THÈSE

En vue de l'obtention du

DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

Délivré par :

Institut National Polytechnique de Toulouse (Toulouse INP)

Discipline ou spécialité :

Ecologie, Biodiversité et Evolution

Présentée et soutenue par :

M. ALLAN RAFFARD
le mardi 8 janvier 2019

Titre :

Rôle écologique de la biodiversité intraspécifique en milieu aquatique

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Ecole doctorale :

Sciences Ecologiques, Vétérinaires, Agronomiques et Bioingénieries (SEVAB)

Unité de recherche :

Laboratoire Ecologie Fonctionnelle et Environnement (ECOLAB)

Directeur(s) de Thèse :

M. SIMON BLANCHET
M. FREDERIC SANTOUL

Rapporteurs :

M. ERIC GARNIER, CNRS MONTPELLIER
Mme ELISA THEBAULT, CNRS PARIS

Membre(s) du jury :

M. THIBAULT DATRY, IRSTEA, Président
M. FREDERIC SANTOUL, UNIVERSITE TOULOUSE 3, Membre
M. JULIEN CUCHEROUSSET, CNRS TOULOUSE, Membre
M. NICOLAS MOUQUET, CNRS MONTPELLIER, Membre
M. SIMON BLANCHET, CNRS TOULOUSE, Membre

Remerciements

Tout d'abord je tiens à remercier Simon Blanchet, mon directeur de thèse. Merci, pour la confiance accordée tout au long de cette thèse, merci de m'avoir toujours poussé à aller au bout de mes idées et merci pour ton optimisme à toute épreuve. Un grand merci également à Julien Cucherousset et Frédéric Santoul. Vous avez toujours été très impliqués dans mes travaux et n'avez jamais été avares en conseils. Merci Julien pour toutes les discussions que nous avons pu avoir. Merci à vous trois pour tout ce que vous avez pu m'apprendre et pour avoir contribué à rendre ces trois années de thèse agréables.

Je remercie également les membres du jury pour avoir accepté mon invitation à participer à ma soutenance de thèse et leur intérêt porté à mes travaux. Merci à Thibault Datry pour avoir présidé ce jury. Je remercie Elisa Thébault et Eric Garnier pour avoir consacré du temps à la lecture de ce manuscrit en tant que rapporteurs. Enfin, merci à Nicolas Mouquet pour avoir participé à mon jury de soutenance et examiné ces travaux.

Merci à tous ceux qui ont participé, de près ou de loin, à mes travaux de thèse. Merci beaucoup à toute l'équipe 'poisson'. Merci à Kéoni pour s'être déplacé dans bien des contrées de France pour aller pêcher des vairons. Merci également à Jérôme et Lisa pour l'aide sur les analyses de données. Je remercie Lucie Di Gesu, Murielle Richard, Alexandre Garreau et Camille Poesy pour leur aide précieuse lors des expériences. Merci également à Remy Lassus Loïc Tudesque et Frédéric Julien pour leur aide lorsque j'en ai eu besoin. Je veux remercier aussi tous les stagiaires qui ont travaillé avec moi : Antoine Fargette, Alix Hervé, Lucas Mignien, Samson Acoca-Pidolle et Yoann Buoro. Merci à Delphine Legrand, José Montoya et Julien Cote pour les conseils, notamment scientifiques, que vous avez pu me donner.

Merci à toutes les personnes qui font que la vie du laboratoire est très agréable. Merci à la 'salle thésard' pour l'ambiance et l'entre-aide : Léa, Lisa, Jérémy, Aisha, Maya, Alexis, Louis et Félix. Merci à Staffan pour toutes les discussions que nous avons eues et pour les petites sorties running, merci également à Félix pour les sorties vélo. Merci aussi à, en vrac, Kéoni, Alice, Eglantine, Robin, Kévin, Jonathan, Jérôme et Anne-Sophie.

Enfin, mes dernières pensées vont à la femme qui partage ma vie et à ma famille, que je remercie de tout mon cœur pour leur soutien sans faille durant ces dernières années.

Avant-propos

Cette thèse a été réalisée au sein de la Station d'Ecologie Théorique et Expérimentale à Moulis et du laboratoire Ecologie Fonctionnelle et Environnement, avec la participation active du laboratoire Evolution et Diversité Biologique. Elle a été financée par une bourse de l'Université Fédérale de Toulouse et de la région Occitanie.

Ce travail de thèse contient une Introduction générale (Chap. I), une partie Modèles d'études (Chap. II), cinq chapitres sous la forme d'articles scientifiques (Chap. III à VII, rédigés en anglais) et une Discussion générale (Chap. VIII). Le chapitre III est publié dans *Biological Reviews.* Le chapitre IV est composé de deux parties ; la première est adaptée d'un article publié dans *Proceedings of the Royal Society B* (article original en ANNEXE 1)*,* la seconde est un article accepté avec des révisions mineures dans *Ecology and Evolution*. Le chapitre VI est en préparation pour soumission dans la revue *Global Change Biology*. Enfin, Les chapitre V et VII sont en préparation pour soumission dans des revues avec comité de lecture.

Résumé

Le déclin actuel de la biodiversité a poussé un grand nombre d'études à s'intéresser aux relations entre la biodiversité et le fonctionnement des écosystèmes. La diversité intraspécifique est une facette centrale de la biodiversité qui permet aux espèces de s'adapter aux variations environnementales et dont l'importance écologique est de plus en plus examinée. A l'aide d'une méta-analyse synthétisant des données sur plusieurs espèces et écosystèmes, nous avons démontré qu'un changement de la diversité intraspécifique peut avoir des conséquences écologiques aussi fortes qu'un changement de la diversité spécifique. Ensuite, au travers d'études empiriques nous avons étudié la diversité fonctionnelle et trophique de populations sauvages de vairons (*Phoxinus phoxinus*), une espèce de poisson abondante en rivière. Une forte variabilité fonctionnelle et trophique a été montrée entre populations de vairons. Cette diversité était structurée de manière complexe du fait de l'action jointe des conditions environnementales, de facteurs évolutifs et des multiples liens existants entre les traits et la niche trophique. Par ailleurs, nous avons montré expérimentalement que les différences fonctionnelles entre populations de vairons pouvaient engendrer des conséquences écologiques aussi fortes qu'une augmentation de la température. De plus, des populations plus diversifiées génétiquement soutenaient des diversités spécifiques élevées puis augmentaient l'intensité des processus écosystémiques. Ces travaux mettent en évidence que la diversité intraspécifique est une composante essentielle de la biodiversité qui doit être considérée comme un facteur majeur affectant la structure des communautés et le fonctionnement des écosystèmes.

Abstract

Current decline of biodiversity has led to many investigations on the relationship between biodiversity and ecosystem functioning. Diversity within species is a pivotal facet of biodiversity that allows species adapting to environmental conditions, and can have ecological effects. Using a meta-analysis synthetizing data across species and ecosystems, we showed that changes in intraspecific diversity can have ecological consequences as strong as changes in species diversity. Then, we empirically studied the functional and trophic diversity among wild populations of European minnows (*Phoxinus phoxinus*), a highly abundant freshwater species. We observed a high functional and trophic variability among populations, which was shaped by environmental conditions, evolutionary factors, and covariations linking traits and trophic niche among each other. Additionally, we experimentally demonstrated that functional variation among populations led to ecological consequences as strong as those of warming ecosystem. Finally, we uncovered that high genetic diversity within population sustained higher species diversity and higher rates of ecosystem processes. Overall, this thesis reveals that intraspecific diversity is a fundamental component of biodiversity that should be considered as a strong driver of community and ecosystem dynamics.

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Chapitre I.

Introduction générale

Depuis la fin du XXe siècle, la conservation de la biodiversité est devenue un enjeu sociétal majeur (Naeem *et al.*, 2009). En effet, la biodiversité permet le maintien de plusieurs services écosystémiques, incluant, parmi d'autres, la séquestration du carbone ou encore la production de ressources (Schmitz *et al.*, 2014; Duffy *et al.*, 2016). En assurant les flux de matières entre niveaux trophiques, la biodiversité permet notamment la structuration et la stabilité des écosystèmes (Thébault & Loreau, 2005; Tilman, Reich, & Knops, 2006). C'est un constituant essentiel du fonctionnement des écosystèmes et donc *in fine* des services écosystémiques. L'un des objectifs des études écologiques est donc de comprendre les interactions entre les organismes et leur environnement, en tenant compte de leurs différences génétiques, taxonomiques, phénotypiques et fonctionnelles. A l'heure où les pressions pesant sur la biodiversité sont multiples (Parmesan, 2006; Daufresne, Lengfellner, & Sommer, 2009; Darimont *et al.*, 2009), la quantification du rôle de la biodiversité dans les écosystèmes est primordiale pour mieux appréhender les conséquences d'une modification de la biodiversité.

I.1. Biodiversité et fonctionnement des écosystèmes

La biodiversité a été historiquement considérée en se basant sur les espèces présentes dans une communauté (Gaston, 1996; Purvis & Hector, 2000; Magurran, 2004). Cette biodiversité est constamment affectée par des causes naturelles (stochasticité environnementale) et par des perturbations d'origine anthropique (Pimm, 1995). Le déclin actuel de la biodiversité a motivé un grand nombre d'études qui se sont penchées sur son importance écologique, faisant émerger des concepts clés (Hooper *et al.*, 2005; Naeem *et al.*, 2009; Cardinale *et al.*, 2012). La biodiversité permet la stabilité et la persistance des communautés et des écosystèmes dans le temps, jouant un rôle de tampon écosystémique (Thébault & Loreau, 2005; Tilman *et al.*, 2006). Cela est dû à la redondance des espèces qui permet de compenser la perte de l'une d'entre elles par une autre qui est fonctionnellement équivalente. En outre, les processus écosystémiques, tels que les taux de production primaire, de décomposition de la matière organique et le recyclage des nutriments, sont dépendants de la diversité d'organismes qui sont présents dans une communauté (Hooper *et al.*, 2005, 2012; Duffy, Godwin, & Cardinale, 2017). Il a été montré que les communautés les plus riches en espèces augmentent l'intensité des processus écosystémiques par rapport aux communautés moins riches (Naeem *et al.*, 1994).

Les relations entre biodiversité et fonctionnement de l'écosystème (B-FE) ont été largement étudiées au niveau interspécifique (Hooper *et al.*, 2005). Ces travaux ont permis de démontrer que les changements de biodiversité ont des effets complexes sur les processus écosystemiques (Naeem & Wright, 2003). En effet, les espèces interagissent fortement entre elles, modulant leurs effets individuels respectifs (de Ruiter, Neutel, & Moore, 1995). Ainsi, les relations B-FE, bien que parfois critiquées et remises en question, peuvent suivre une relation saturante où une augmentation de la biodiversité entraîne une augmentation du processus écosystémique considéré (p. ex. la production primaire) jusqu'à atteindre un plateau (Hooper *et al.*, 2005). Cette forme est due à plusieurs mécanismes complémentaires. A de faible valeur de diversité, une augmentation de la biodiversité cause une augmentation (ou un changement de taux) du processus écosystémique par complémentarité/facilitation entre espèce (Cardinale, Palmer, & Collins, 2002; Downing & Leibold, 2002). Par exemple, un partage des nutriments rend les espèces plus performantes et induit une plus forte productivité primaire. De plus, un effet 'échantillonnage' peut augmenter la probabilité d'inclure une espèce clé (Wardle, 1999). Ensuite, à de fortes valeurs de diversité, il y a une plus forte probabilité que plusieurs espèces occupent des fonctions similaires, alors les changements n'ont plus (ou peu) d'effets à cause de la redondance fonctionnelle entre espèces (Wardle, Bonner, & Nicholson, 1997; Cadotte, Carscadden, & Mirotchnick, 2011).

Il apparaît alors judicieux de s'intéresser aux traits *fonctionnels* des espèces. Les traits fonctionnels ont été définis comme les caractéristiques phénotypiques des organismes (i) leur permettant de répondre aux variations environnementales (*traits réponses*), et/ou (ii) décrivant leurs influences sur le fonctionnement des écosystèmes (*traits d'effets*) (Lavorel & Garnier, 2002; Violle *et al.*, 2007; Díaz *et al.*, 2013). La diversité fonctionnelle a alors l'avantage de prédire les processus écosystémiques en se basant sur ce que les espèces font réellement dans un écosystème (Mcgill *et al.*, 2006; Petchey & Gaston, 2006). Quantifier la diversité fonctionnelle améliore les capacités de prédictions du fonctionnement des écosystèmes par rapport à l'identité spécifique (Tilman *et al.*, 1997; Gagic *et al.*, 2015). En étant liés aux capacités physiologiques et trophiques des individus, les traits d'effets peuvent moduler les relations entre organismes dans un réseau trophique et donc les flux de nutriments dans l'écosystème (Woodward *et al.*, 2005). Plusieurs types de traits d'effets ont été caractérisés et permettent d'inférer les impacts écosystémiques des organismes. Chez les producteurs primaires les traits physiologiques et morphologiques sont les plus importants pour moduler les processus écosystémiques (Cornelissen *et al.*, 2003). Les traits morphologiques impliquent majoritairement la taille des organes. Par exemple, la surface spécifique des feuilles chez les plantes influence leur capacité à capter la lumière et donc la production primaire (Garnier *et al.*, 2004). Les traits physiologiques, comme le contenu en nutriments (azote et phosphore) ou en lignine, peuvent influencer les communautés d'herbivores ou le recyclage des nutriments (Bardgett & Wardle, 2003). Chez les consommateurs, les traits d'effets impliquent leurs capacités trophiques, locomotrices, et physiologiques. Les consommateurs les plus hauts dans la chaîne trophique induisent principalement des effets « top-down ». Ainsi, les traits trophiques et locomoteurs déterminent l'acquisition de ressources, laquelle influence la biomasse des échelons trophiques inferieurs et les flux de nutriments du bas vers le haut des chaînes trophiques (Norkko *et al.*, 2013; Rudolf *et al.*, 2014). Les traits physiologiques des organismes, comme les taux métabolique et d'excrétion, peuvent affecter directement la quantité de nutriment (p. ex. azote) dans un milieu, et donc indirectement la production primaire (Vanni, 2002; Schmitz, Hawlena, & Trussell, 2010). Les consommateurs plus bas dans les chaînes trophiques peuvent également induire des effets « bottom-up ». Ces effets inclus principalement les capacités d'évitement de la prédation qui pourraient moduler la biomasse des échelons trophiques supérieurs.

I.2. Diversité intraspécifique

Non-seulement la biodiversité peut être quantifiée selon la variabilité taxonomique, phylogénétique et fonctionnelle des espèces au sein d'une communauté, mais également selon la variabilité génétique, phénotypique et fonctionnelle retrouvée entre individus d'une même espèce (Bolnick *et al.*, 2003; Violle *et al.*, 2012). Cette diversité intraspécifique a historiquement été étudiée en évolution, car elle représente la base grâce à laquelle les espèces s'adaptent face aux variations environnementales et subsistent dans le temps (Darwin, 1859). La sélection naturelle, la dérive génétique, les mutations et la plasticité phénotypique sont autant de mécanismes qui façonnent la diversité phénotypique. La part de la diversité intraspécifique dans les communautés est loin d'être négligeable, puisqu'il a été montré que, chez des communautés de plantes, la part de la variance attribuable à la diversité intraspécifique pouvait atteindre jusqu'à 25% de la variation phénotypique totale (Siefert *et al.*, 2015). Il s'avère alors important de comprendre les effets écologiques de la diversité intraspécifique et les mécanismes la générant afin de mieux appréhender le fonctionnement des écosystèmes.

I.2.1. Déterminants de la diversité intraspécifique

La diversité intraspécifique a été historiquement étudiée pour comprendre l'évolution des espèces (Darwin, 1859). Cette diversité est en effet la base grâce à laquelle les espèces s'adaptent et évoluent face aux aléas environnementaux. La diversité intraspécifique est portée par les gènes qui produisent des phénotypes qui sont cruciaux pour déterminer la valeur sélective (« fitness », en anglais) des individus. Plusieurs mécanismes, agissant indépendamment ou en interaction peuvent créer des différenciations génétiques/phénotypiques entre populations et modifier la richesse génétique/phénotypique des populations. Dans cette partie une liste non-exhaustive des concepts généraux qui déterminent la diversité intraspécifique est dressée.

Facteurs évolutifs : Sélection, flux de gènes et dérive génétique

Tout d'abord, les phénotypes des organismes peuvent être sélectionnés. Un prérequis pour cela est que le trait en question soit héritable (Darwin, 1859; Roff, 1992). Au fil des générations la sélection naturelle peut générer des populations ayant différents phénotypes (Kingsolver & Pfennig, 2007). Très brièvement, les individus ayant la meilleure valeur sélective dans un environnement donné peuvent transmettre leurs gènes, et les traits phénotypiques résultants, à leur descendance et *in fine* à la population. Le phénotype sélectionné donne un avantage aux individus (c.-à-d. valeur sélective) qui le portent et cet avantage est grandement dépendant des conditions biotiques et abiotiques dans lesquelles vivent les individus. Ainsi, des populations vivant dans des habitats différents peuvent diverger sélectivement, et présenter des phénotypes/niches différents. Les individus sont alors souvent adaptés à leur environnement local, c'est-à-dire que les individus sont plus performants dans l'habitat dans lequel ils ont été sélectionnés que dans un autre habitat avec des caractéristiques environnementales différentes (Kawecki & Ebert, 2004; Blanquart *et al.*, 2013). De nombreuses recherches ont étudié la sélection naturelle sur de nombreux traits phénotypiques (Endler, 1986; Kingsolver *et al.*, 2001). Un des exemples types de sélection est celui du mélanisme chez la phalène du bouleau (*Biston betularia*) en Angleterre. Ces papillons présentent habituellement une couleur claire, mais dans les zones industrielles les individus plus sombres ont été sélectionnés car cela leur procuraient un avantage face à la prédation (c.-à-d. le camouflage). La fréquence des individus sombres dans les populations des zones industrielles a alors augmenté aboutissant à des populations avec un mélanisme élevé (Kettlewell, 1983). Alternativement, si un milieu n'impose pas de contraintes fortes, alors plusieurs phénotypes peuvent subsister. Cela mène à des populations plus riches (c.-à-d. forte richesse intraspécifique) en comparaison à des milieux ou un seul phénotype aurait l'avantage.

Les flux de gènes entre populations peuvent aussi affecter la diversité génétique des populations (Slatkin, 1985; Sexton, Hangartner, & Hoffmann, 2014). Ces flux sont déterminés par la migration des individus d'une population à une autre. Il a été décrit qu'une forte immigration pouvait augmenter la richesse génétique des populations due à l'apport de 'nouveaux' gènes par les migrants venant de populations extérieures. La connectivité des populations les unes aux autres est l'un des facteurs pouvant affecter le niveau de dispersion entre populations (Paz-Vinas *et al.*, 2015). Ainsi, les populations les plus centrales et connectées dans un réseau de populations sont plus riches génétiquement, à l'inverse de populations plus isolées (c.-à-d. moins connectées, Eckert, Samis, & Lougheed, 2008; Alp *et al.*, 2012).

Dans les populations les plus isolées avec de petits effectifs, la dérive génétique peut avoir un rôle important à jouer (Lande, 1976). La dérive est une force évolutive majeure qui décrit les changements aléatoires des fréquences alléliques dans une population. Dans les populations de petites tailles la richesse génétique (p.ex. le nombre d'allèle) est réduite car la dérive génétique fixe les allèles les plus communs. En effet, si un allèle est représenté en faible proportion alors il a d'autant plus de chance d'être perdu par le fait du hasard si la population est de petite taille (Lande, 1976; Hartl & Clark, 1997). Donc la dérive génétique est un facteur essentiel pouvant réduire la richesse génétique des populations. Aussi, c'est un processus qui peut, avec le temps, créer des divergences entre populations (Leinonen *et al.*, 2013). Si les gènes modifiés sont liés à un ou des traits phénotypiques alors un changement de phénotype s'opère. Par exemple, sous certaines conditions empêchant la dispersion des individus et donc le flux de gène, la masse corporelle peut varier significativement entre populations sous l'action de la dérive génétique (Johansson, Primmer, & Merilä, 2007).

Facteurs externes : plasticité, influence environnementale

Les facteurs environnementaux biotiques et abiotiques peuvent aussi moduler l'expression des phénotypes en induisant de la plasticité. La plasticité se définie lorsqu'un seul génotype produit plusieurs phénotypes selon le contexte environnemental (Hendry, 2016). Les organismes s'adaptent alors aux facteurs environnementaux au cours de leur vie (DeWitt, Sih & Wilson, 1998). Autrement dit, selon les conditions de développement et l'environnement dans lequel ils se trouvent, les individus peuvent exprimer des phénotypes différents. Les réponses sont très nombreuses et dépendent de l'organisme, du trait et du facteur environnemental considérés. Les traits physiologiques, comme le taux métabolique, peuvent répondre à des changements de prédation, température et de disponibilité en ressources (Hawlena & Schmitz, 2010; Burton *et al.*, 2011). Le comportement des individus peut être aussi plastique. Par exemple, le comportement alimentaire des daphnies (*Daphnia magna*) change selon la pression de prédation ; en présence d'un prédateur elles occupent une place différente dans la colonne d'eau afin d'éviter la prédation (De Meester, 1996). La morphologie aussi est dépendante de l'environnement dans lequel se développent les organismes leur permettant d'être plus performant. Les poissons peuvent ainsi développer des morphologies différentes selon la vitesse d'écoulement de l'eau des rivières pour minimiser les pertes énergétiques (Pakkasmaa & Piironen, 2000; Imre, McLaughlin, & Noakes, 2002). Les ressources disponibles entraînent également des changements de morphologies afin d'en optimiser l'acquisition (Hutchings & de Kroon, 1994; Day & McPhail, 1996). Tous ces changements phénotypiques peuvent s'accompagner de modifications des besoins nutritifs, et donc de régimes alimentaires (Rosenblatt & Schmitz, 2016). Ainsi, des variations environnementales, en modulant le métabolisme des organismes, modifient également leurs besoins en azote, phosphore et carbone pour soutenir ce métabolisme (Schmitz, 2013; Rosenblatt & Schmitz, 2016). Une augmentation de la température peut induire une augmentation du taux métabolique, les individus peuvent alors adapter leur régime alimentaire vers des ressources plus riches en carbone pour soutenir une respiration plus élevée (Boersma *et al.*, 2016).

Covariations entre traits : les syndromes

Enfin, les traits ne dépendent pas seulement de l'environnement et du génotype des individus, mais ils dépendent aussi les uns des autres au travers des covariations existantes entre eux (Armbruster *et al.*, 2014). La variation d'un trait peut alors dépendre de la variation d'autres traits. Les traits sont en effet impliqués dans de multiples covariations, et cet ensemble de covariations entre plusieurs traits se définie comme un *syndrome* (Dingemanse *et al.*, 2007). Plusieurs syndromes ont été étudiés historiquement sur différents types de traits incluant les traits d'histoire de vie (Roff, 1992), comportementaux (Sih, Bell, & Johnson, 2004) et de dispersion (Clobert *et al.*, 2009). Plus récemment un syndrome de 'rythme de vie' (« pace-of-life syndrome », en anglais) a été décrit entre plusieurs types de traits incluant l'histoire de vie, le comportement, la physiologie et la morphologie des individus (Reale *et al.*, 2010; Mittelbach *et al.*, 2014). Par exemple, le taux métabolique peut être corrélé avec des traits comportementaux tel que l'activité, et des traits d'histoire de vie tel que la croissance (Zavorka *et al.*, 2017). Ces syndromes résultent de mécanismes complexes impliquant la pléiotropie (c.-à-d. les gènes qui gouvernent l'expression de plusieurs traits), les besoins énergétiques, et/ou l'allométrie (Hoffmann & Merilä, 1999; Hildrew *et al.*, 2007; Careau *et al.*, 2008). Les syndromes peuvent aussi être variables entre populations à cause des variations environnementales (Peiman & Robinson, 2017). Comme l'environnement exerce des contraintes sur les traits, il peut également moduler les relations entre eux (Killen *et al.*, 2013; Peiman & Robinson, 2017). Par exemple, un manque de nourriture peut induire une corrélation entre le comportement de prise de risque et le taux métabolique, alors qu'en présence de nourriture ces deux traits ne sont pas corrélés (Killen, Marras, & McKenzie, 2011). Il est donc important de prendre en compte les covariations entre traits, et les syndromes résultants, afin de mieux comprendre comment se forme la diversité intraspécifique.

I.2.2. Impacts écologiques de la diversité intraspécifique

Alors que la diversité intraspécifique a souvent été ignorée en écologie, lors des deux dernières décennies, des travaux ont montré son importance pour l'évaluation du fonctionnement des écosystèmes (Whitham *et al.*, 2003, 2006; Bailey *et al.*, 2009). L'idée que la diversité intraspécifique puisse affecter l'environnement vient de plusieurs champs de recherche clés. Tout d'abord, la génétique des communautés et des écosystèmes propose que les variations génotypiques des individus peuvent se répercuter sur la structure des communautés et le fonctionnement des écosystèmes (Whitham *et al.*, 2006, 2008). Ensuite, le principe de construction de niche stipule que -en occupant des niches différentes- les individus au sein d'une même espèce peuvent façonner leur environnement, ce qui peut modifier en retour leur valeur sélective (Odling-Smee, Laland, & Feldman, 2003; Odling-Smee *et al.*, 2013; Matthews *et al.*, 2014). En effet, les individus au sein d'une espèce peuvent occuper des niches écologiques différentes (Bolnick *et al.*, 2003) conduisant à des effets sur la structure des communautés et le fonctionnement des écosystèmes au travers de plusieurs mécanismes. Jusqu'à présent les conséquences écologiques de la diversité intraspécifique ont été principalement testées expérimentalement en considérant deux aspects : (i) la *richesse* intraspécifique décrivant des différences de nombres de génotypes/phénotypes entre populations, et (ii) la *variation* intraspécifique décrivant les différentiations moyennes génotypiques/phénotypiques des populations (Figure I.1).

Richesse intraspécifique : intraspécifique B-FE

Tout d'abord, des études se sont intéressées aux différences de *richesse* génétique/phénotypique entre populations (Figure I.1a). En effet, des populations d'une même espèce peuvent présenter des nombres de génotypes/phénotypes différents. La richesse intraspécifique peut affecter le fonctionnement des écosystèmes et générer des relations entre biodiversité intraspécifique et le fonctionnement des écosystèmes (iB-FE, Hughes et al., 2008). Les relations iB-FE font un parallèle avec la théorie et les mécanismes développés initialement au niveau interspécifique (Hughes et al., 2008). Ces idées s'appliquent au niveau des populations, où les plus riches peuvent engendrer une augmentation des taux des processus écosystemiques par rapport aux populations les moins riches du fait des interactions entre différents génotypes/phénotypes.

Principalement de manière expérimentale, un certain nombre de travaux ont démontré des effets « bottom-up » de la richesse intraspécifique chez les producteurs primaires en manipulant la richesse génotypique de populations expérimentales. Plusieurs génotypes, à condition qu'ils génèrent des traits d'effets différents, peuvent se partager les ressources (p. ex. les nutriments) et avoir une croissance plus forte, de laquelle peut résulter une plus forte production primaire (Fridley & Grime, 2010). Le taux de décomposition et le recyclage des nutriments sont également affectés par la richesse intraspécifique. Par exemple, des mixtures de feuilles de plusieurs génotypes se décomposent plus rapidement que des feuilles venant d'un seul génotype car elles présentent une diversité nutritive plus importante pour les décomposeurs (Crutsinger, Sanders, & Classen, 2009; Wang *et al.*, 2014). Cette décomposition rapide peut également générer un relargage de nutriments plus important dans l'environnement (Crutsinger *et al.*, 2009; Wang *et al.*, 2014). En plus d'affecter les processus écosystemiques, la richesse intraspécifique peut également avoir des effets sur la structure des communautés (Vellend & Geber, 2005; Bailey *et al.*, 2009; Koricheva & Hayes, 2018). Encore une fois, la présence de plusieurs génotypes dans une population permet une complémentarité fonctionnelle favorisant la diversité à l'échelle des communautés (Figure I.1a). Ainsi, les communautés d'invertébrés sont plus diversifiées, et l'abondance des individus est plus grande, en présence de populations de plantes plus riches génétiquement (Crawford & Rudgers, 2013; Abbott *et al.*, 2017). En effet, les populations les plus riches peuvent fournir une plus grande quantité de niches aux invertébrés, en terme de ressource (palatabilité des génotypes) et d'habitat (morphologie des génotypes) que les populations les moins riches (Johnson, Lajeunesse, & Agrawal, 2006).

En comparaison, relativement très peu d'études se sont intéressées aux effets « top-down » de la richesse intraspécifique chez des espèces de consommateurs. En manipulant la variance en taille (c.-à-d. un trait fortement lié aux capacités trophiques) des individus dans des populations d'amphibiens (*Lithobates sylvaticus*), une étude a démontré des impacts sur les communautés de proies en mésocosmes (Carlson & Langkilde, 2017). La richesse intraspécifique chez les consommateurs pourrait alors exercer un contrôle sur la diversité et l'abondance des échelons trophiques inferieurs. Cependant, ce résultat n'est pas consistant puisque d'autres travaux n'ont pas montré de tels effets sur les communautés ni sur les processus écosystémiques (Hargrave, Hambright, & Weider, 2011; Ingram, Stutz, & Bolnick, 2011). Ces résultats contrastés ne permettent pas de généralisation et font apparaître le besoin de nouvelles études s'intéressant aux effets écologiques de la richesse intraspécifique chez les consommateurs.

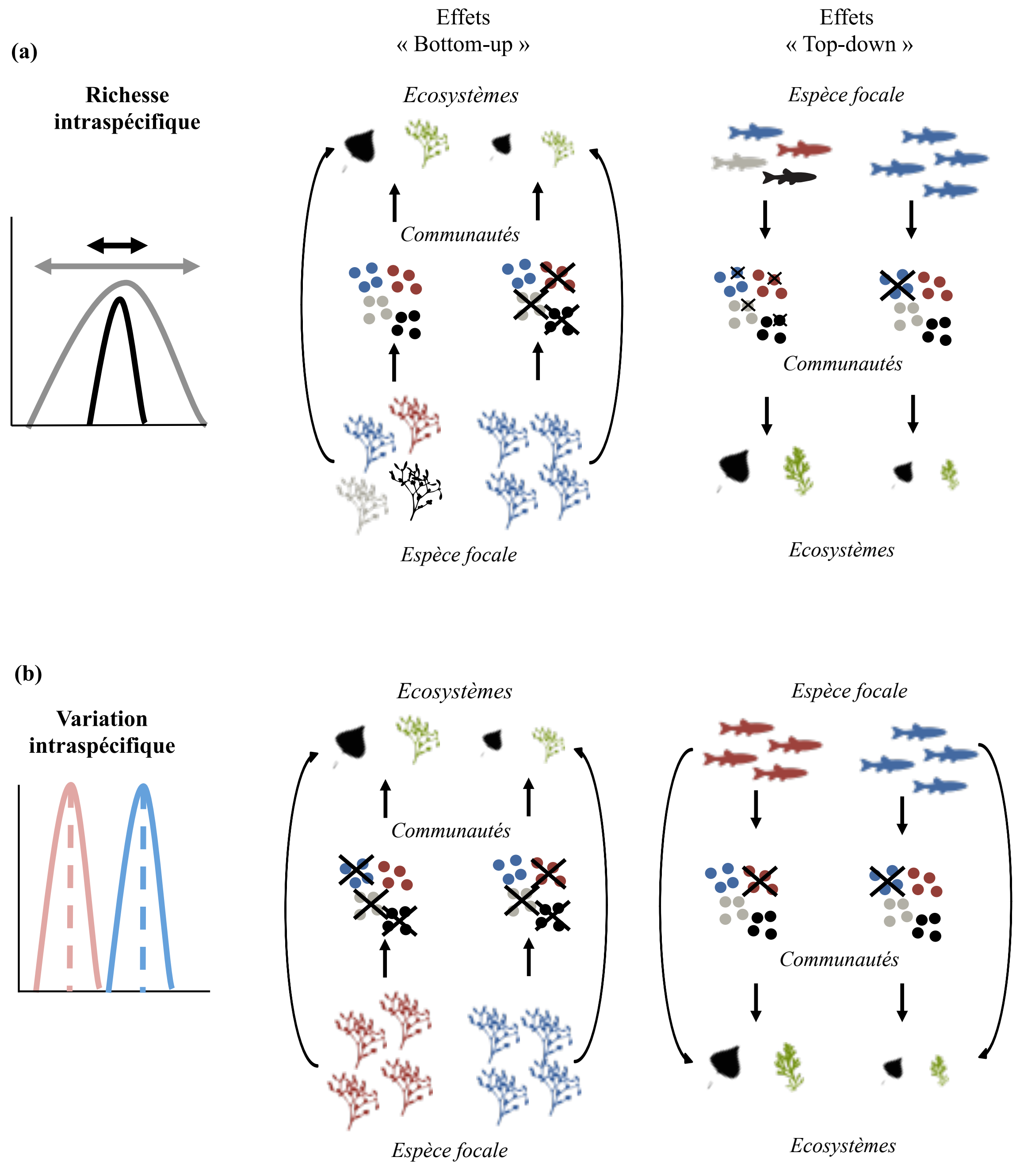


Figure I.1. La richesse **(a)** et la variation **(b)** intraspécifique sont deux facettes importantes de la diversité intraspécifique. Des populations avec des richesses élevées mènent à des communautés plus riches, et augmentent les taux des processus écosystémiques **(a)**. Complémentairement, des populations avec des traits différents mènent à des communautés et écosystèmes différents **(b)**. Ces effets sont moins prévisibles car ils sont fortement dépendants de l'identité de la population. Les couleurs de l'espèce focale représentent des traits différents, les couleurs des points représentent des taxons différents. La taille des symboles écosystémiques représente les taux des processus.

Variation intraspécifique : de la différenciation des populations aux divergences écosystémiques

Les effets écologiques de la diversité intraspécifique ne se mesurent pas seulement avec la richesse des populations, mais également avec les *variations* des génotypes/phénotypes entre les populations (Figure I.1b). Des populations avec des génotypes/phénotypes différents peuvent aussi être fonctionnellement différentes. Ainsi, la variation intraspécifique entre populations (et même entre individus) peut affecter les communautés et les processus écosystémiques (Des Roches *et al.*, 2018).

Les effets peuvent d'abord être trophiques. Les populations de producteurs primaires peuvent différer dans leur efficacité d'acquisition des nutriments, ou avoir des palatabilités variables, induites par des contenus chimiques variables (p. ex. lignine) entraînant des effets sur les communautés d'herbivores en favorisant un certain type de consommateurs (Barbour *et al.*, 2009; Crutsinger *et al.*, 2014). Ces effets peuvent ensuite se répercuter en cascade sur les autres échelons trophiques (Terborgh & Estes, 2010). De la même manière les consommateurs peuvent induire des pressions différentes sur leurs proies selon leur régime trophique (Post *et al.*, 2008). Des traits comme la taille corporelle, le taux métabolique ou la morphologie, peuvent varier entre populations et sont importants pour déterminer les besoins énergétiques et nutritifs des individus (Brown *et al.*, 2004; Hildrew, Raffaelli, & Edmonds-Browns, 2007). Des populations ayant des traits différents peuvent affecter les communautés d'invertébrés à cause de la sélectivité trophique des individus (Harmon *et al.*, 2009; Howeth *et al.*, 2013). Par exemple, des coléoptères (*Plagiodera versicolora*) avec des préférences alimentaires variables peuvent affecter la structure des communautés en impactant l'abondance relative de leurs proies (Utsumi, 2015). Le fonctionnement des écosystèmes est aussi dépendant des effets trophiques des individus ; soit indirectement via les effets sur les communautés, soit directement. Les effets directs apparaissent essentiellement lorsque les organismes en question sont étroitement liés à un processus. Les consommateurs tels que les herbivores, les décomposeurs et les prédateurs peuvent affecter respectivement la production primaire, le taux de décomposition et la biomasse des organismes (Alp et al., 2016; Rudolf and Rasmussen, 2013; Walsh et al., 2012). Par exemple, une variation du taux de croissance entre populations de daphnies (*Daphnia ambigua*) peut se répercuter sur la production primaire car les populations avec une forte croissance consomment plus de phytoplanctons (Walsh *et al.*, 2012).

En outre, la variation intraspécifique peut induire des conséquences écologiques non trophiques. Celles-ci impliquent principalement une modification des nutriments présents dans le milieu qui peut se répercuter sur les processus écosystémiques (Schmitz *et al.*, 2010). La composition en nutriments (c.-à-d. stoechiométrie) des organismes, principalement en azote et en phosphore, est de plus en plus étudiée car elle est fortement liée à la production primaire et au taux de décomposition (Leal, Seehausen, & Matthews, 2016). Le taux de décomposition est dépendant, entre autre, de la composition en nutriments de la matière organique (Gessner, Chauvet, & Dobson, 1999). Des variations de stoechiométrie entre populations peuvent donc induire des taux différents de décomposition (Madritch, Donaldson, & Lindroth, 2006; Lecerf & Chauvet, 2008; Hawlena *et al.*, 2012). Selon que les communautés de décomposeurs soient limitées en azote ou en phosphore, la concentration de l'un ou l'autre de ces nutriments sera la plus importante. De la même façon les nutriments sont importants pour la production primaire (Bassar *et al.*, 2012; Evangelista *et al.*, 2017). Ces effets peuvent être dépendants de la décomposition qui entraîne un relargage des nutriments, alors disponibles pour les producteurs primaires. Aussi, le taux d'excrétion de nutriments par les consommateurs, issu de mécanismes cataboliques et homéostatiques, est important pour prédire les effets de la variation intraspécifique sur les écosystèmes (Vanni, 2002; Schmitz *et al.*, 2010). En effet, la variation d'excrétion entre populations d'une même espèce peut être assez grande pour engendrer des taux de production primaire différents (Bassar *et al.*, 2010). Par exemple, des individus excrétant une grande quantité de phosphore entraînent une augmentation de la production primaire par rapport aux individus ayant une faible excrétion de phosphore (Evangelista *et al.*, 2017).

Malgré de nombreux travaux et des résultats forts, l'implication de la variation intraspécifique pour la structure des communautés et le fonctionnement des écosystèmes comparé aux grandes forces environnementales est encore assez méconnue. L'importance écologique de la biodiversité au niveau interspécifique a déjà été relativisée par rapport à des facteurs atmosphériques et climatiques, démontrant qu'elle ne devait pas être négligée (Hooper *et al.*, 2012). Aussi, il est important de connaître l'implication relative d'une modification de la variation intraspécifique pour de futures prédictions sur les dynamiques de la biosphère.

I.2.3. Dynamiques éco-évolutives

Ainsi un nombre croissant d'études a fait émerger l'importance la diversité intraspécifique à la fois pour le fonctionnement des écosystèmes et pour l'adaptation des espèces (Thompson, 1998; Fussmann, Loreau, & Abrams, 2007; Schoener, 2011). La diversité intraspécifique se place alors au centre des relations entre processus écologiques et évolutifs (Hendry, 2016) (Figure I.2). Les interactions réciproques et contemporaines entre ces processus définissent des dynamiques éco-évolutives (Pelletier, Garant, & Hendry, 2009; Schoener, 2011). Celles-ci se produisent lorsque des facteurs écologiques affectent la diversité intraspécifique par des processus évolutifs (p.ex. sélection) mais aussi lorsque la diversité intraspécifique (due aux processus évolutifs) affectent les facteurs écologiques (des populations aux écosystèmes) (Fussmann *et al.*, 2007). Ces dynamiques (c.-à-d. de l'écologie à l'évolution et de l'évolution à l'écologie) peuvent être indépendantes ou cycliques générant alors des boucles de rétroactions éco-évolutives. Elles se produisent lorsque la diversité intraspécifique affecte les processus écologiques et que ces modifications écologiques sont assez grandes pour devenir de nouvelles pressions de sélection modulant l'évolution des organismes.

Récemment, ces boucles de rétroactions éco-évolutives ont été démontrées expérimentalement sur les pucerons (*Mysus persicae*) et les épinoches (*Gasterosteus aculeatus*) (Turcotte, Reznick, & Daniel Hare, 2013; Matthews *et al.*, 2016; Brunner *et al.*, 2017; Best *et al.*, 2017). Chez les épinoches, deux populations suisses, vivant en lac (lac Constance) et dans une rivière se déversant dans le lac, ont été étudiées. Il a été montré que ces populations ont divergé sélectivement ; les individus vivant en milieu lacustre étaient adaptés phénotypiquement (c.-à-d. morphologie, couleurs,…) à la vie limnétique, alors que les individus venant de la rivière étaient adaptés à la vie en eau courante (Lucek, Sivasundar, & Seehausen, 2012). Les deux phénotypes ont été décrits comme des écotypes. Ces écotypes ont été répliqués dans des mésocosmes aquatiques afin de tester leurs effets écologiques et évolutifs subséquents. Dans un premier temps les différentes populations ont mené à des communautés et des écosystèmes divergents, notamment par l'abondance du zooplancton et la biomasse algale. Dans un second temps ces divergences écologiques ont affecté l'évolution d'une nouvelle génération d'épinoches en favorisant des génotypes différents (Matthews *et al.*, 2016). Dans ce contexte les traits d'effets sont cruciaux car, ce sont à travers eux que les individus affectent les processus écologiques (Lavorel & Garnier, 2002; Violle *et al.*, 2007). L'évolution de la variabilité des traits fonctionnels est alors importante à prendre en compte pour pouvoir quantifier l'effet de l'évolution sur les communautés et le fonctionnement des écosystèmes (Matthews *et al.*, 2011).

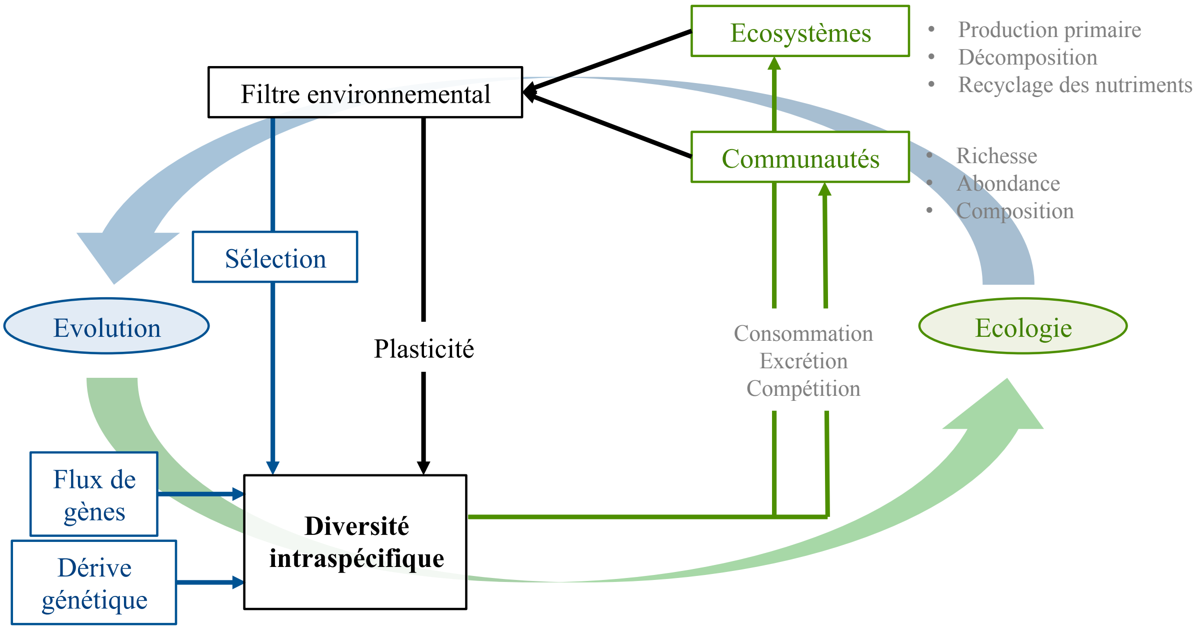


Figure I.2. Schéma conceptuel des causes et des conséquences de la diversité intraspécifique pouvant mener à des dynamiques éco-évolutives. Les modifications sur les communautés et les écosystèmes peuvent jouer le rôle de filtre environnemental modifiant la diversité intraspécifique. Ces modifications peuvent avoir lieu à une échelle de temps biologique par la plasticité, ou évolutive par la sélection naturelle. Les flux de gènes et la dérive génétique sont deux autres facteurs évolutifs affectant la diversité intraspécifique. Note : l'effet des mutations sur la diversité intraspécifique, et l'effet de la diversité intraspécifique sur les populations font aussi partie des dynamiques éco-évolutives mais ne sont pas montrés.

I.3. Ecosystèmes aquatiques

Les écosystèmes aquatiques, parmi lesquels se trouvent les lacs et les rivières, ne représentent qu'une infime fraction de l'eau présente sur la Terre (0,01%). Cependant, ces écosystèmes abritent une grande biodiversité puisque plus de 100 000 espèces y ont été décrites, ce qui représente environ 6% de la biodiversité totale de la planète (Dudgeon *et al.*, 2006). Cette grande biodiversité concentrée dans de faibles espaces font des écosystèmes aquatiques des 'points chauds' de biodiversité (Strayer & Dudgeon, 2010). Ainsi, des producteurs primaires aux prédateurs, tous les niveaux des réseaux trophiques présentent une forte diversité (Nelson, Grande, & Wilson, 1994; Covich *et al.*, 2004a; Clarke *et al.*, 2008; Stomp *et al.*, 2011). Elle est primordiale pour le fonctionnement des écosystèmes et *in fine* pour soutenir de nombreux services écosystemiques (Covich *et al.*, 2004a, 2004b). Ceux-ci profèrent une forte valeur socio-économique aux écosystèmes aquatiques (Pearce, 1998; Dudgeon *et al.*, 2006). En effet, la biodiversité aquatique est importante pour (i) l'approvisionnement en ressources (p. ex. les saumons et les écrevisses, Beamish & Bouillon, 1993; Holdich, 1993), (ii) l'assainissement de l'eau en régulant le recyclage et le stockage des nutriments (Cardinale, 2011), ou encore (iii) pour les loisirs récréatifs comme la pêche (Pitcher & Hollingworth, 2008).

Malgré leur importance à de multiples points de vue, les écosystèmes aquatiques font face à de nombreuses pressions. La pollution, la surexploitation, les invasions biologiques, le changement climatique et la dégradation des habitats sont autant de pressions qui pèsent sur la biodiversité aquatique et menacent le fonctionnement des écosystèmes (Dudgeon *et al.*, 2006; Leprieur *et al.*, 2008; Strayer & Dudgeon, 2010; Vörösmarty *et al.*, 2010). Les espèces introduites de poissons, par exemple, peuvent causer des extinctions d'espèces et des changements de composition des communautés au niveau local (Cucherousset & Olden, 2011). Ces pressions sont aussi responsables de modifications de la diversité intraspécifique (Mimura *et al.*, 2016). Tout d'abord des changements au niveau génétique peuvent être détectés en réponse aux perturbations anthropiques (Hoffmann & Willi, 2008), comme le ré-empoissonnement (Prunier *et al.*, 2018). Ces modifications génétiques peuvent être accompagnées de modifications phénotypiques et ultimement des modifications fonctionnelles peuvent avoir lieu. Par exemple, une espèce envahissante peut monopoliser une ressource et causer des changements de régime alimentaire des espèces natives (Cucherousset *et al.*, 2007). Ces changements à l'échelle intraspécifique peuvent alors se répercuter sur les écosystèmes aquatiques (Palkovacs *et al.*, 2018), renforçant le besoin de comprendre le rôle de la diversité intraspécifique dans ces milieux.

I.3.1. Fonctionnement particulier

Les écosystèmes aquatiques présentent plusieurs particularités. En terme physique tout d'abord, la viscosité de l'eau, deux fois plus élevée que celle de l'air, leurs confère des propriétés physiques et écosystemiques différentes. C'est donc un milieu porteur où les organismes et les nutriments se repartissent dans tout le volume d'eau. Les groupes fonctionnels sont les mêmes qu'en milieux terrestres (producteurs primaires, décomposeurs, herbivores, prédateurs), mais la base des réseaux trophiques est occupée à la fois par les producteurs primaires aquatiques (biofilms et macrophytes) et par la matière allochtone terrestre (Wetzel, 1995). Les apports de matières terrestres sont élevés notamment du fait de la faible surface des milieux aquatiques, entourés de terres, et fournissent une grande quantité de nutriment aux milieux aquatiques (Bartels *et al.*, 2012). Cette matière allochtone est principalement représentée par des débris végétaux, et a façonné la biodiversité puisqu'elle soutient tout un réseau trophique. Ainsi, les producteurs primaires aquatiques et la matière allochtone soutiennent deux réseaux trophiques qui sont liés par les consommateurs généralistes et le recyclage des nutriments (Vanni, 2002). Une autre particularité notable des écosystèmes aquatiques concerne l'importance des consommateurs. Il a été proposé que les effets « top-down » sur les réseaux trophiques et les processus écosystémiques étaient exacerbés en milieu aquatique (Shurin *et al.*, 2002; Shurin, Gruner, & Hillebrand, 2006). Très brièvement, plusieurs facteurs peuvent expliquer ce pattern : un ratio élevé entre la taille des consommateurs et celle des producteurs primaires, ou encore une meilleure qualité nutritive des producteurs primaires (Elser *et al.*, 2000; Chase, 2000; Shurin *et al.*, 2002). Cela confère aux consommateurs une importance écologique accrue dans les écosystèmes aquatiques.

D'autre part, les écosystèmes aquatiques sont structurés singulièrement (c.-à-d. en îlot pour les lacs et en réseaux pour les rivières) induisant une organisation particulière de la biodiversité. Spécialement, les rivières incluent des nœuds et des branches formant une structure en réseau dendritique, dans laquelle l'écoulement de l'eau est contraint directionnellement par l'altitude (Grant, Lowe, & Fagan, 2007). Les organismes sont dépendants de la structure de ces réseaux, et la biodiversité est plus élevée au niveau des confluences, lieu de connections entre deux branches (Altermatt, 2013). De l'amont à l'aval, les cours d'eau se rejoignent en des rivières de plus en plus grandes avec des caractéristiques biotiques et abiotiques différentes (Vannote *et al.*, 1980). Ces caractéristiques incluent principalement la physico-chimie de l'eau, la diversité d'habitats, le type de sédiment et la quantité de matière végétale allochtone. Ce gradient abrite des communautés avec des diversités fonctionnelles différentes. Ainsi, les décomposeurs/détritivores très présents en amont, du fait de la forte couverture végétale, sont remplacés par des organismes filtreurs et brouteurs en aval (Vannote *et al.*, 1980). La diversité intraspécifique est aussi affectée par la structure dendritique des rivières (Paz-Vinas & Blanchet, 2015). Notamment, les flux de gènes vers les populations avales sont favorisés par l'écoulement de l'eau. Ainsi, les populations sont plus riches génétiquement en aval, et les populations en amont sont plus soumises à la dérive génétique (Alp *et al.*, 2012; Paz-Vinas *et al.*, 2015). Enfin, le phénotype et le régime alimentaire des individus peuvent varier entre populations subissant des pressions environnementales différentes sur le réseau (Zandonà *et al.*, 2017; Fourtune *et al.*, 2018), rendant les populations fonctionnellement différentes.

I.3.2. Modèles privilégiés

Enfin, les écosystèmes aquatiques ont été le théâtre de nombreux travaux s'intéressant au rôle écologique de la diversité intraspécifique, faisant émerger de nouveaux concepts forts. Ces études ont notamment cherché à comprendre si les processus évolutifs, modulant la variation intraspécifique, pouvait générer des dynamiques éco-évolutives en affectant la structure des communautés et le fonctionnement des écosystèmes (Palkovacs *et al.*, 2015; Matthews *et al.*, 2016). Ainsi, plusieurs traits et caractéristiques au niveau intraspécifique ont été étudiés expérimentalement et montrés comme importants pour les écosystèmes. Par exemple, l'histoire de vie des individus peut influencer le phénotype individuel et se répercuter sur les fonctions écosystémiques comme le recyclage des nutriments (Bassar *et al.*, 2010; El-Sabaawi *et al.*, 2015). Aussi, la variation de la taille des individus chez les organismes aquatiques est essentielle pour déterminer le fonctionnement des écosystèmes (Rudolf & Rasmussen, 2013a, b). En utilisant principalement l'épinoche (*G. aculeatus*) comme modèle d'étude, il a été démontré que des populations avec différentes morphologies ont des effets différents sur les communautés d'invertébrés et le fonctionnement de l'écosystème (Harmon *et al.*, 2009; Des Roches *et al.*, 2013; Best *et al.*, 2017). Ces études expérimentales sont appuyées par des études ayant observé des effets écologiques de la variation intraspécifique en milieu naturel. Il a été montré que la variabilité des traits d'effets entre populations de gaspareau (*Alosa pseudoharengus*), vivant dans différents lacs d'Amérique du nord, pouvait se répercuter sur la composition des communautés de zooplancton et de phytoplancton (Post *et al.*, 2008; Howeth *et al.*, 2013).

I.4. Objectifs

Cette thèse a pour principal objectif de comprendre comment les individus au sein des espèces varient dans leur milieu naturel afin d'évaluer l'implication de cette variabilité pour le fonctionnement des écosystèmes aquatiques. Nous avons couplé des approches méta-analytique, observationnelle et expérimentale afin d'intégrer des notions globales, descriptives et mécanistes dans l'évaluation du rôle écologique de la diversité intraspécifique. Pour les parties empiriques, nous avons utilisé un petit poisson d'eau douce, le vairon commun (*Phoxinus phoxinus*), comme espèce modèle en se focalisant sur des populations échantillonnées dans des rivières au sein du bassin de la Garonne (*Chapitre II*).

La thèse se structure en trois principaux objectifs et cinq chapitres.

Le premier objectif était dédié à une synthèse globale des effets écologiques de la diversité intraspécifique. Ainsi, le *Chapitre III* de cette thèse est une méta-analyse visant à déterminer les conséquences de la diversité intraspécifique sur la structure des communautés et le fonctionnement des écosystèmes. Nous avons donc fait une revue quantitative, au travers de plusieurs espèces et écosystèmes, des effets écologiques de la variation et de la richesse intraspécifique.

Le deuxième objectif était de quantifier la diversité intraspécifique selon différents aspects et d'explorer les potentiels déterminants de cette diversité. Les traits fonctionnels et les niches trophiques ont été visés car c'est au travers d'eux que la diversité intraspécifique affecte les communautés et les écosystèmes. Tout d'abord, nous avons étudié les syndromes entre traits fonctionnels et leur variation entre plusieurs populations de vairons. Nous avons testé si les traits et leurs corrélations étaient dépendants de paramètres environnementaux, adaptatifs et/ou phylogénétiques (*Chapitre IV*). Ensuite, nous nous sommes intéressés à la variabilité trophique, quantifiée à l'aide d'une analyse des isotopes stables, entre populations de vairons. Nous avons testé si les traits fonctionnels (ici la morphologie des poissons), et les paramètres environnementaux pouvaient expliquer la variabilité trophique du vairon (*Chapitre V*).

Le troisième objectif était de mesurer expérimentalement les effets écologiques de la variation et de la richesse intraspécifique. Tout d'abord, nous avons quantifié l'importance relative des effets éco-évolutifs induits par la *variation* intraspécifique avec les effets d'un facteur abiotique fort : la température (*Chapitre VI*). Pour cela nous avons mis en place une expérience en deux étapes afin de quantifier les effets (i) écologiques et (ii) évolutifs subséquents de la variation intraspécifique (entre six populations de vairons) et d'un changement de température de 2°C. Enfin, nous avons testé si la *richesse* intraspécifique pouvait moduler les effets « top-down » sur la structure des communautés et les processus écosystémiques. Nous avons manipulé, en mésocosmes, la richesse et la structure fonctionnelle (composition en traits fonctionnels) d'assemblages expérimentaux de vairons afin d'évaluer leurs effets sur la structure des communautés de proies et sur le fonctionnement des écosystèmes (*Chapitre VII*).

Chapitre II.

Modèles d'études

Espèce modèle : le vairon commun

Les chapitres IV à VII de cette thèse ont été effectués en utilisant le vairon commun (*Phoxinus phoxinus*) en tant que modèle d'étude (Figure II.1). C'est une espèce de la famille des cyprinidés (Cyprinidae), dont les individus sont de petites tailles, mesurant de 3 à 8 cm (dépassant rarement 10 cm), et vivent de manière grégaire (Frost, 1943; Freyhof & Kottelat, 2008). Les vairons atteignent leur maturité sexuelle vers 2 ans, et vivent ordinairement entre 4 et 5 ans. Ils se reproduisent généralement au printemps et en été lorsque les températures dépassent les 15-17°C. Les vairons vivent dans des eaux bien oxygénées et se sont adaptés à la vie dans les rivières et dans les lacs (notamment les lacs de montagne en France). La distribution de cette espèce est vaste puisque des vairons peuvent être trouvés à travers toute l'Europe (Freyhof & Kottelat, 2008), et sont très abondants en France (Keith *et al.*, 2011). Le vairon est une espèce plutôt généraliste, se nourrissant de macro-invertébrés benthiques, de periphyton et même de proies limnétiques comme du zooplancton (Frost, 1943).

Scientifiquement le vairon est une espèce relativement peu étudiée en comparaison aux espèces modèles classiques (p.ex. épinoche, *G. Aculeatus*, ou poisson zèbre, *Danio rerio*) et aux espèces ayant une forte valeur socio-économique (p.ex. les salmonidés). Les travaux se sont majoritairement intéressés au comportement d'évitement de la prédation (p.ex. Magurran & Pitcher, 1987; Magurran, 1990, 2010). Outre le comportement, de la variabilité morphologique a aussi été montrée entre populations de vairons. Notamment, des différences morphologiques ont été observées entre différents lacs, ou entre lacs et rivières, et il a été montré que ces différences morphologiques étaient probablement adaptatives (Collin & Fumagalli, 2011, 2015). Cependant, ces différences morphologiques étaient moins marquées entre populations venant de rivières différentes (Fourtune *et al.*, 2018). Malgré la faible variabilité morphologique, les différenciations génétiques entre populations étaient élevées (Fourtune *et al.*, 2018), suggérant que la variabilité phénotypique pouvait être nichée dans d'autres traits. Nous avons alors quantifié la variabilité phénotypique des vairons en mesurant la masse corporelle, le taux métabolique, le taux d'excrétion et le comportement dans le Chapitre IV ; la niche trophique et la morphologie (en utilisant une approche morphométrique basée sur des ratios, alors que les précédents travaux ont étudié les déformations en se basant sur des points de repères) dans le Chapitre V. Enfin, il est intéressant de noter que le vairon n'est pas 'neutre' écologiquement puisque son introduction dans certains lacs, où il était originellement absent, a impacté la structure des communautés d'espèces locales (Museth *et al.*, 2007; Miró, Sabás, & Ventura, 2018; Gacia *et al.*, 2018).

Sites d'études : les rivières du bassin Dordogne-Garonne

Les populations étudiées lors de cette thèse ont été échantillonnées dans des rivières du bassin versant Dordogne-Garonne, dans le sud-ouest de la France. Vingt-et-une rivières au total ont été sélectionnées, dont 13 ont été étudiées dans le Chapitre IV, 12 dans le Chapitre V, 6 dans le Chapitre VI et 10 dans le Chapitre VII (Figure II.1). Ces rivières été connues par l'équipe de recherche (Fourtune *et al.*, 2016, 2018) pour présenter des conditions environnementales variées. Globalement, ce sont des rivières tempérées, présentant des températures estivales variant de 15,5°C à 21,5°C. Elles avaient également des profils différents puisqu'elles faisaient de 4 m à 80 m de largeur et étaient à des altitudes différentes (150 m à 750 m). Les principaux prédateurs des vairons dans ces cours d'eau sont les truites fario (*Salmo trutta*), et dans certaines rivières des brochets (*Esox Lucius*), des truites arc-en-ciel (*Oncorhynchus mykiss*), des perches (*Perca fluviatilis*), ou encore des sandres (*Sander lucioperca*) peuvent être présents. Cette variabilité environnementale permet ainsi de maximiser les possibilités de saisir la diversité intraspécifique entre les populations de vairons. En effet, ces conditions environnementales - parmi d'autres - sont connues pour imposer des contraintes physiologiques pouvant moduler le phénotype (Gillooly, 2001; Biro, Beckmann, & Stamps, 2010; Bestion *et al.*, 2015).

Les échantillonnages ont été effectués en pêche électrique (appareil DK 7000) pour toutes les rivières étudiées. C'est une méthode de pêche active qui permet de minimiser les biais phénotypiques liés à l'échantillonnage par rapport aux méthodes de captures passives (Biro & Dingemanse, 2009). Chaque rivière a été échantillonnée de la même façon. Sur chaque rivière nous avons pêché sur un tronçon de 200 m afin d'avoir un échantillon de vairons le plus représentatif possible de la population. Grâce à une estimation visuelle de la taille moyenne des poissons récoltés, seulement les poissons adultes ont été échantillonnés. Les précisions sur les tailles d'échantillons sont disponibles dans les différents chapitres. Les pêches électriques ont été effectuées grâce à des arrêtés préfectoraux délivrés par les directions départementales des territoires de l'Ariège, l'Aveyron, la Corrèze, la Haute-Garonne, les Hautes-Pyrénées, le Lot, le Tarn, et le Tarn-et-Garonne.

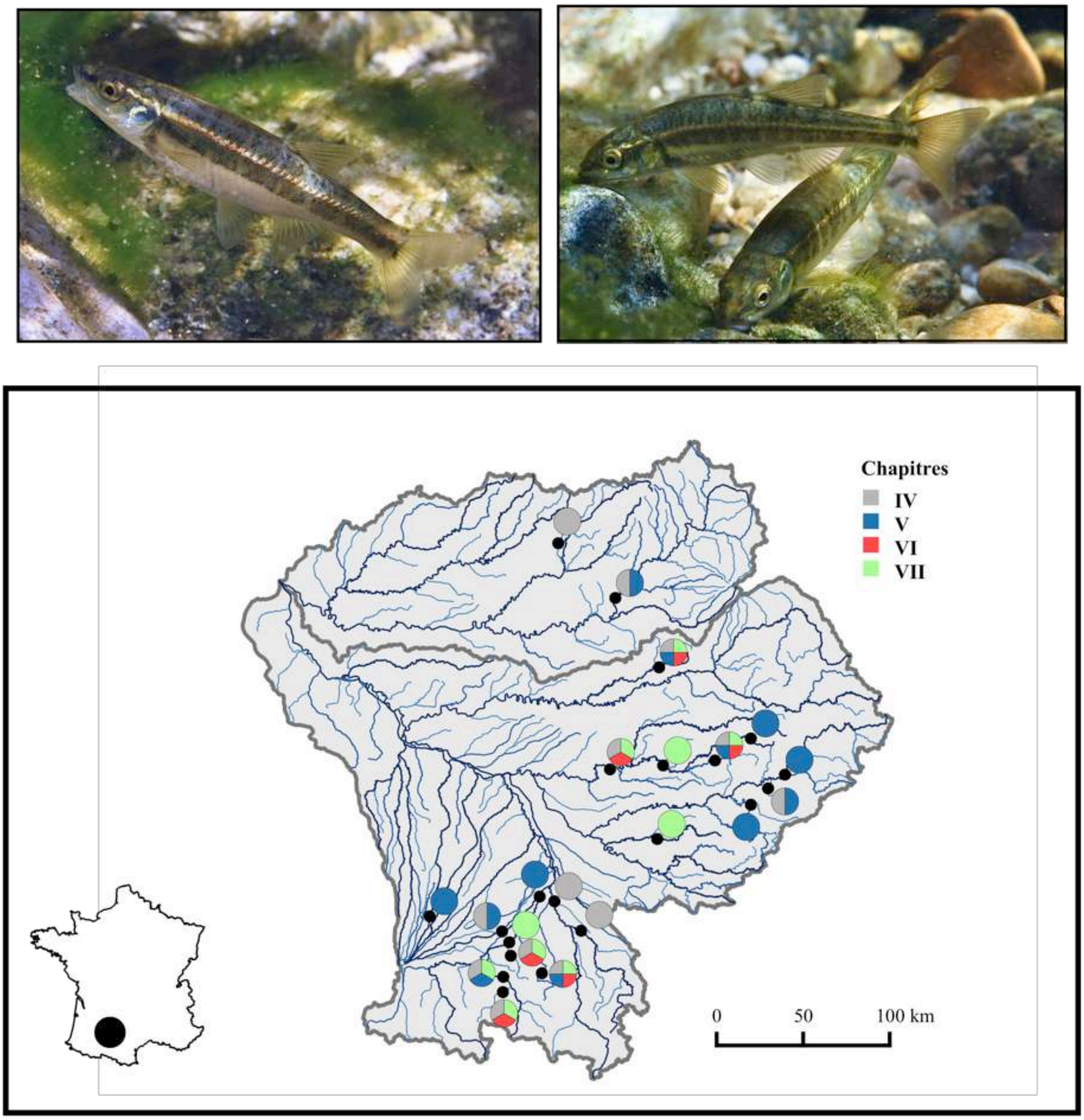


Figure II.1. Photos de vairons adultes dans le Tarn (prises par Gaël Grenouillet). La carte indique la distribution géographique des 21 rivières échantillonnées durant cette thèse et leurs utilisations dans les différents chapitres observationnels (IV et V) et expérimentaux (VI et VII).

Chapitre III.

The community and ecosystem consequences of intraspecific diversity: a meta-analysis

Allan Raffard[1,2], Frédéric Santoul[2], Julien Cucherousset[3], & Simon Blanchet[1,3]

[1] CNRS, Université Toulouse III Paul Sabatier, Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UMR-5321, 2 route du CNRS, F-09200 Moulis, France

[2] EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France.

[3] Laboratoire Évolution et Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, IRD, UPS, 118 route de Narbonne, Toulouse 31062, France

Manuscript published in **Biological Reviews**.

Résumé

La compréhension des liens entre la biodiversité et le fonctionnement des écosystèmes a des implications majeures. Ces relations ont généralement été étudiées au niveau interspécifique. Cependant, la diversité intraspécifique est de plus en plus perçue comme une facette importante de la biodiversité. Ici, nous avons fait une synthèse quantitative testant, au travers de plusieurs espèces, si la diversité intraspécifique pouvait être un facteur essentiel influençant la structure des communautés et le fonctionnement des écosystèmes. Plus précisément, nous avons testé (i) si le nombre de génotypes/phénotypes (c.-à-d. la *richesse* intraspécifique) et l'identité des génotypes/phénotypes (c.-à-d. la *variation* intraspécifique) dans les populations affectaient la structure des communautés et les fonctions écosystémiques, (ii) la force de ces effets écologiques, et (iii) si ces effets variaient entre groupes taxonomiques et entre différentes réponses écologiques. Les résultats ont mis en évidence une relation saturante entre la richesse intraspécifique et les dynamiques écologiques. Il est important de noter que la richesse intraspécifique affectait les dynamiques écologiques avec une force égale à celle de la richesse spécifique. Nos résultats ont aussi montré, sur plus de 50 espèces, que la variation intraspécifique avait des effets écologiques deux fois supérieurs à ceux attendues par le hasard, et qu'ils avaient pu être précédemment sous-estimés. Enfin, les effets écologiques de la variation intraspécifique étaient plus forts quand la variation était manipulée chez les producteurs primaires plutôt que chez les consommateurs, et quand les effets étaient mesurés au niveau des écosystèmes plutôt qu'au niveau des communautés. En résumé, nous avons montré que la variation et la richesse intraspécifique étaient importantes pour la structure des communautés et le fonctionnement des écosystèmes, révélant le rôle majeur de la biodiversité au sein des espèces pour la compréhension des dynamiques écologiques.

Abstract

Understanding the relationships between biodiversity and ecosystem functioning has major implications. Biodiversity–ecosystem functioning relationships are generally investigated at the interspecific level, although intraspecific diversity (i.e. within-species diversity) is increasingly perceived as an important ecological facet of biodiversity. Here, we provide a quantitative and integrative synthesis testing, across diverse plant and animal species, whether intraspecific diversity is a major driver of community dynamics and ecosystem functioning. We specifically tested (i) whether the number of genotypes/phenotypes (i.e. intraspecific *richness*) or the specific identity of genotypes/phenotypes (i.e. intraspecific *variation*) in populations modulate the structure of communities and the functioning of ecosystems, (ii) whether the ecological effects of intraspecific richness and variation are strong in magnitude, and (iii) whether these effects vary among taxonomic groups and ecological responses. We found a non-linear relationship between intraspecific richness and community and ecosystem dynamics that follows a saturating curve shape, as observed for biodiversity–function relationships measured at the interspecific level. Importantly, intraspecific richness modulated ecological dynamics with a magnitude that was equal to that previously reported for interspecific richness. Our results further confirm, based on a database containing more than 50 species, that intraspecific variation also has substantial effects on ecological dynamics. We demonstrated that the effects of intraspecific variation are twice as high as expected by chance, and that they might have been underestimated previously. Finally, we found that the ecological effects of intraspecific variation are not homogeneous and are actually stronger when intraspecific variation is manipulated in primary producers than in consumer species, and when they are measured at the ecosystem rather than at the community level. Overall, we demonstrated that the two facets of intraspecific diversity (richness and variation) can both strongly affect community and ecosystem dynamics, which reveals the pivotal role of within-species biodiversity for understanding ecological dynamics.

Introduction

Understanding the relationships between biodiversity and ecosystem functioning is an intensely active field of research informing on the services provided by biodiversity (Chapin *et al.*, 2000; Loreau, 2000; Hooper *et al.*, 2005; Cardinale *et al.*, 2012). Biodiversity is generally quantified as the taxonomic, functional and/or phylogenetic diversity of a species assemblage, and most studies on biodiversity–ecosystem functioning relationships have to date focused on the interspecific facet of biodiversity (Naeem *et al.*, 1994; Downing & Leibold, 2002; Hillebrand & Matthiessen, 2009). However, biodiversity also includes an intraspecific facet that is defined as the phenotypic, functional and genetic diversity measured within a single species (Odling-Smee, Laland & Feldman, 2003; Bolnick *et al.*, 2003). During the last two decades, intraspecific diversity has been demonstrated to account for a non-negligible part of the total biodiversity measured in plants and animals (Fridley & Grime, 2010; de Bello *et al.*, 2011), representing in some cases up to a quarter of the total variability measured in communities (Fridley & Grime, 2010; de Bello *et al.*, 2011; Siefert *et al.*, 2015).

In parallel, the hypothesis that intraspecific diversity may affect ecological dynamics at levels higher than the population level (for instance the composition and the dynamics of communities and/or the dynamics of ecosystem functions) has been conceptualized (Bolnick *et al.*, 2003, 2011; Hughes *et al.*, 2008; Bailey *et al.*, 2009; Violle *et al.*, 2012). These conceptual insights have been validated by several key experiments both in plants and animals (Whitham *et al.*, 2003; Madritch, Greene & Lindroth, 2009; Matthews *et al.*, 2016; Rudman & Schluter, 2016). For instance, the experimental manipulation of fish phenotypes from several evolutionarily independent populations has been shown to generate significant changes in both the community structure of invertebrate prey and the primary productivity of the ecosystem (Harmon *et al.*, 2009; Matthews *et al.*, 2016).

Intraspecific diversity can be characterized based on the *richness* of populations, which corresponds to the differences in the number of genotypes and/or phenotypes composing populations. For instance, populations are often characterized according to their ‘allelic, genotypic or phenotypic richness’, which is a population parallel of species richness, a common metric measured at the interspecific level and classically used to investigate biodiversity–ecosystem function (BEF) relationships (Crutsinger *et al.*, 2006). Intraspecific richness can also affect ecological dynamics hence generating ‘intraspecific BEF’ (Whitham *et al.*, 2006; Crutsinger *et al.*, 2006). The basic hypothesis for intraspecific BEF is that increasing the number of genotypes/phenotypes in a population should alter (either negatively or positively) key ecological functions such as the decomposition rate of organic matter or the structure of communities. For instance, experiments manipulating the number of genotypes (from one to 12 genotypes) in plant (*Solidago altissima*) populations have shown that richer populations contained a higher diversity of invertebrates (Crutsinger *et al.*, 2006). Actually, the ecological consequences of intraspecific richness should follow a saturating curve (i.e. a rapid increase followed by a plateau) as often described for BEF observed at the interspecific level (Hughes *et al.*, 2008). Although rarely tested empirically, this saturating shape could be due to the combined effects of several mechanisms. Populations with different richness could have different ecological consequences because of ecological complementarity among genotypes/phenotypes (i.e. niche partitioning, facilitation occurring when genotypes use different resources), inhibition among genotypes/phenotypes (when multiple genotypes are in competition for resources), or functional redundancy among genotypes/phenotypes that can make populations ecologically equivalent (Johnson, Lajeunesse & Agrawal, 2006; Hughes *et al.*, 2008). Yet, the shape of the relationship between intraspecific richness and ecological dynamics has rarely been investigated empirically and to our knowledge has never been quantified across species.

The ecological consequences of intraspecific diversity can also be investigated through the lens of *variation* in genotypic or phenotypic attributes. Adaptive and non-adaptive evolutionary processes such as natural selection, plasticity or genetic drift can generate unique phenotypic differences among populations. These differences can be associated to key functional processes such as food acquisition or nutrient cycling (e.g. Grant & Grant, 2006; Rudgers & Whitney, 2006; Lowe, Kovach & Allendorf, 2017), resulting in both trophic and non-trophic effects of intraspecific variation on ecological dynamics (Odling-Smee *et al.*, 2003; Whitham *et al.*, 2003; Matthews *et al.*, 2011). For instance, it has been shown experimentally that plant genotypes differing in their susceptibility to herbivores harbour different communities of herbivores (Crutsinger, Cadotte & Sanders, 2009*a*; Barbour *et al.*, 2009*b*). Similarly, mesocosm experiments have shown that differences in diet within predator populations can modify prey community structure (Post *et al.*, 2008; Harmon *et al.*, 2009; Howeth *et al.*, 2013). Non-trophic interactions can also have an important role. For instance, differences in the chemical composition of individuals can result in differences in excretion rate or in leaf chemistry that can then affect ecosystem functions such as primary production or nutrient recycling (Lecerf & Chauvet, 2008; El-Sabaawi *et al.*, 2015). Recently, Des Roches *et al.* (2018) demonstrated that intraspecific variation can affect ecological dynamics to the same extent as the removal or replacement of a species in the environment. Although based on a relatively limited number of studies (25 studies on 15 species), their study confirmed the hypothesis that intraspecific variation might be a non-negligible driver of ecological dynamics.

Here, we investigated – across various species and ecosystems – the extent to which both intraspecific richness and intraspecific variation affect the structure of communities and the functioning of ecosystems, and whether intraspecific diversity is a major driver of ecological dynamics. We reviewed published studies testing the causal effects of intraspecific diversity on ecological dynamics in two meta-analyses synthesizing published data across taxa and ecosystems for intraspecific richness and variation, respectively, and to fulfil three specific objectives. First, we tested the significance and the shape of the relationship between intraspecific richness and ecological dynamics. We expected to find a significant saturating relationship between intraspecific richness and ecological dynamics, because of potential facilitation and functional redundancy among genotypes and phenotypes (Hughes *et al.*, 2008). Second, we tested whether manipulating intraspecific richness has similar effects on ecological dynamics to manipulating interspecific richness, by comparing the ecological effects of intraspecific richness with those of interspecific richness obtained from experimental studies manipulating species richness (Duffy, Godwin & Cardinale, 2017). Finally, we provided a novel and extensive quantitative synthesis testing for the effects of intraspecific variation on ecological dynamics. Des Roches *et al.* (2018) previously focused on studies removing or replacing the target species (by which intraspecific variation was manipulated) to investigate the ecological consequences of intraspecific variation. This strongly restricted the number of available studies for which effects sizes could be calculated, and potentially upwardly biased the resulting estimates (Des Roches *et al.*, 2018). We here relax this restriction by considering all studies manipulating intraspecific variation, and use a null-model approach to provide a more accurate relative effect size of intraspecific variation on ecological dynamics. We also built on this extended data set to partition variance in the ecological consequences of intraspecific variation according to the type of organism manipulated and the type of response variable measured. We tested whether the magnitude of the effects of intraspecific variation on ecological dynamics vary among organism types (primary producers *versus* consumers) and levels of biological organization (community *versus* ecosystem levels). Because primary producers form the basis of trophic chains, we expect stronger ecological effects of intraspecific variation in producers than in consumers.

We also expect stronger effects of intraspecific variation on ecosystem functions than on metrics describing community structure because ecosystem functions are affected by both trophic and non-trophic effects of biodiversity (Matthews *et al.*, 2014).

Materials and methods

Data collection

We compiled data from published articles quantifying the effects of intraspecific diversity in a single species on community structure and/or ecosystem functioning. We focused only on intraspecific diversity that represented the integrative phenotypic effect of multiple evolutionary processes including selection, drift and/or plasticity. As a result, we did not consider articles focusing on experimentally induced intraspecific diversity through induced plastic responses to particular predatory or environmental cues [for example see Werner & Peacor (2003) for a review]. We reviewed several experimental studies manipulating intraspecific variation and/or richness within a single species to test their respective ecological effects. We also reviewed some observational studies with strong biological hypotheses and adequate design allowing inferring causal links from intraspecific diversity to ecological dynamics (e.g. Post *et al.*, 2008). Studies varying intraspecific diversity within a set of multiple species (e.g. Booth & Grime, 2003) were not included in this meta-analysis. The literature search was carried out using the ISI *Web of Knowledge* and *Scopus* platforms (last accessed 25th July 2018). We also scrutinized the reference list of each article to obtain additional articles. The following key words were used in various combinations: *community genetics* AND *intraspecific variation*, *eco-evolutionary dynamics* AND *ecosystem function*, *community genetics* AND *ecosystem function*, and *intraspecific genetic variation* AND *ecosystem function*. We selected articles describing the effects of genotypic and/or phenotypic richness (intraspecific *richness*) and/or different genotypes/phenotypes (intraspecific *variation*) in a single target species on community and/or ecosystem dynamics. A total of 90 studies with available statistics were selected (Appendix III.S1 and Figure III.S1). Among these, 23 studies (100% experimental studies) focused on intraspecific richness and 75 studies (90% experimental studies, 10% empirical studies) focused on intraspecific variation.

For each study, we recorded the Latin name of the target species and classified them as primary producers or consumers (including primary and secondary consumers as well as predators) and according to the major taxonomic categories represented in our data sets:

arthropods (8 species), fishes (6 species), herbaceous plants (14 species), trees (31 species), and fungi (5 species). Overall, this led to 51 species for studies focusing on intraspecific variation, and 17 species for studies focusing on intraspecific richness. We recorded seven main response variables related to community structure and ecosystem functioning. A community is here defined as a group of at least two species, and we focused on three types of response variables describing the structure of communities: (1) species abundance: total number of individuals of all species; (2) biomass: total mass of individuals of all species; (3) community structure: number of species (e.g. Simpson or Shannon indices), species evenness and/or species richness.

Regarding response variables at the ecosystem level, we considered four main ecosystem functions: (1) decomposition rate: rate at which organic matter is recycled; (2) elemental cycling: quantity of organic or inorganic materials; (3) primary productivity: measured as several proxies of primary producers: biomass of primary producers excluding the productivity of the target species, chlorophyll *a* concentration, daily oxygen production, and photosynthetically active radiation; (4) ecosystem respiration: rate of oxygen consumption.

Meta-analysis

The ecological consequences of intraspecific richness

To test for the consequences of intraspecific richness on ecological dynamics, we focused only on studies investigating the consequences of genotypic richness since this was the intraspecific diversity facet most commonly manipulated to test for the effects of intraspecific richness on ecological dynamics. Here, we used the log-transformed response ratio ($\ln RR$) as an effect size. $\ln RR$ was computed as: $\ln\left(\frac{XG}{1G}\right)$, where *1G* is the average of the response variable measured for the treatment with a single genotype (i.e. monoculture), and *XG* is the average of the response variable measured for each treatment independently including more than one genotype. For each response variable, $\ln RR$ increases as the difference in the mean response variable measured in the treatment with a single genotype and treatments including more than one genotype increases. We also recorded the difference in the number of genotypes between the single genotype treatment (monoculture) and all other treatments separately (i.e. treatments including 2–12 genotypes) as the ‘difference in intraspecific richness’. In our data set, difference in intraspecific richness therefore varied between one and

11 genotypes. This approach allowed quantifying the ecological consequences of increasing the number of genotypes for each target species. Since each study generally assessed the effects of intraspecific richness on more than one response variable, our data set included a total of 135 assays.

We wanted to test the shape and the significance of the relationship between ln*RR* and the difference in intraspecific richness across all case studies. The general expectation is that ecological differences between treatments increase as differences in intraspecific richness increase, although this increase may be non-linear (Hughes *et al.*, 2008). We therefore used non-linear mixed-effect models to test the significance and shape of the relationship between absolute values of ln*RR* (|ln*RR*|) and differences in intraspecific richness. More precisely, we modelled this relationship using four different models to determine the most likely shape of the relationship between |ln*RR*| and difference in intraspecific richness: (1) a null model (one parameter) was computed for the null-effect hypothesis (i.e. no significant relationship between |ln*RR*| and difference in intraspecific richness); (2) a linear model (two parameters) suggesting a positive and linear relationship between |ln*RR*| and difference in intraspecific richness; (3) a Michaelis–Menten model (two parameters) in which |ln*RR*| increases with intraspecific richness, until a plateau is reached (saturating shape); (4) an asymptotic exponential model (two parameters) with a shape similar to the Michaelis–Menten model, except that the plateau is reached sooner.

All models cited above included article ID and the monoculture ID (i.e. the monoculture treatment to which each other treatment of richness was compared for a given response variable within each study) as random terms to account for non-independence of effect sizes (Noble *et al.*, 2017), and the inverse of the sample size as a weighting parameter giving greater weight to articles including more replicates. Models were compared using the Akaike information criterion (AIC) and we retained (as “best models”) all models that fell within a $\Delta AIC < 4$ (Burnham & Anderson, 2002). We also calculated for each model the Akaike weight that provides a conditional probability for each model to be best supported by the data (Burnham & Anderson, 2002).

We then compared the magnitude (absolute effect size) of ecological effects of intraspecific and interspecific richness. We extracted from each study and for each response variable the ln*RR* corresponding to the most extreme levels of genotypic richness (x_{max}) manipulated in each study ($N = 63$ ln*RR*). These values were subsequently compared to published ln*RR* values calculated following a similar method for experiments ($N = 35$)

manipulating interspecific richness (Duffy *et al.*, 2017). Because absolute effect sizes follow a folded-normal distribution, we used an 'analyse and transform' approach (*sensu* Morrissey, 2016*a,b*) to estimate the absolute means of effect sizes. This approach consists first of estimating the mean and variance of ln*RR* (using non-absolute values), and then deriving the mean absolute value from these estimates. To do so, we estimated the mean of ln*RR* for interspecific and intraspecific richness, respectively, using two independent intercept models with ln*RR* as the response variable, article ID as the random effect and the inverse of the sample size as the weighting parameter. These intercept models were implemented using the MCMCglmm package in R (Hadfield, 2010). Markov chain Monte Carlo (MCMC) chains were run on 15×10^5 iterations, with a burn-in interval of 3×10^4, a thinning interval of 1×10^3, and an inverse-Wishart prior ($V = 1$ and $\eta = 0.002$). Finally, the estimated means' ln*RR* values were converted into absolute-magnitude |ln*RR*| values (following Morrissey, 2016*b*), and we compared the magnitudes of the ecological effects of interspecific and intraspecific richness based on visual inspection of 95% percentile intervals (PIs).

Finally, to compare the ecological consequences of intraspecific richness between levels of biological organization, we performed the same 'analyse and transform' approach described above. We used a linear mixed-effect model (implemented in the MCMCglmm package in R, and parameterized similarly than above) with the ln*RR* as the dependent variable, the inverse of the sample size as the weighting parameter, article ID and monoculture ID as random factors, and with the level of biological organization (community *versus* ecosystem response variables) treated as a fixed effect. The type of organism was not included in this analysis given that studies on intraspecific richness focused almost exclusively on primary producers (with two exceptions on fungi).

The ecological consequences of intraspecific variation

Given that most studies (86%) did not include a control (i.e. a treatment without the target species), we compared the strength of effects among all unique genotypes and/or phenotypes that were considered in each study. Studies generally compared the consequences of 2–10 different unique genotypes and/or phenotypes (i.e. 2–10 treatments, with each treatment corresponding to a unique genotype/phenotype) on community and/or ecosystem dynamics; we gathered from each study the statistic (t, F, *Chi*-squared, Pearson's r, Spearman's r, R^2 or Hedges' g) associated with the between-treatments comparison (i.e. the variation of the phenotypes/genotypes). The higher the absolute value of the statistic, the higher the community and ecosystem consequences due to the variation of genotypes and/or phenotypes. The value of each statistic was converted into a correlation coefficient (r) ranging from 0 to 1 (see Table IIII.S1 for the formulae used). We did not use the direction of the statistic (i.e. positive or negative) because this depended upon the ecological response variable that was considered, which complicates comparisons on the direction of effects. The Z-Fisher transformation then was used to obtain a standardized effect size using the formula: $Zr = 0.5\ln\frac{(1+r)}{(1-r)}$. For each Zr value, we calculated the corresponding standard error as $se_{Zr} = \frac{1}{\sqrt{n-3}}$ (Nakagawa & Cuthill, 2007). Since each study generally focused on more than one response variable, we obtained a total of 502 observed Zr values, each corresponding to the effect size of intraspecific variation observed within one species on a single response variable. The mean global Zr or mean effect size observed ($\mathrm{MES_{obs}}$) and its 95% confidence interval (CI) were calculated using an intercept-only model. This intercept-only model was run as a mixed model with no fixed effect, article ID as the random effect and se_{Zr} included as a weighting parameter to give more weight to studies with a larger sample size (Koricheva, Gurevitch & Mengersen, 2013).

Because Zr ranged between 0 and $+\infty$, the CIs of the $\mathrm{MES_{obs}}$ do not theoretically overlap 0, which makes it difficult to assess the significance of the strength of the $\mathrm{MES_{obs}}$. We therefore used a null-model approach to test if $\mathrm{MES_{obs}}$ was significantly different from that expected under the null hypothesis, i.e. the true effect of intraspecific variation in all studies was zero. We resampled each statistic (e.g. t, F) from each empirical study in their respective null distribution with the adequate degree of freedom. This resampled set of statistics (N = 502) was transformed into Zr as described above to create a set of resampled Zr values. We used this set of resampled Zr values to fit an intercept-only model with no fixed effect, the corresponding article ID as a random term and se_{Zr} included as a weighting parameter (as for $\mathrm{MES_{obs}}$). The mean global resampled Zr ($\mathrm{MES_{res}}$) was extracted from the model, and we repeated this resampling procedure 1000 times to obtain 1000 values of $\mathrm{MES_{res}}$. This resampled distribution of 1000 $\mathrm{MES_{res}}$ approximates the range of possible MES values expected if the null hypothesis was true. Finally, we calculated the probability of $\mathrm{MES_{obs}}$ to be larger than expected under this null hypothesis using a one-tailed test (Manly, 1997).

We then compared the median of effect sizes ($\mathrm{MES_{common}}$) of studies that were in common between our extended data set and that used by Des Roches *et al.* (2018) (i.e. 15

studies that were used both in our meta-analysis and that of Des Roches *et al.*) to a selection of 15 studies randomly sampled from our extended data set (i.e. 75 studies in our extended data set). We calculated the median effect size for the subset of random studies ($\mathrm{MES}_{\mathrm{ran}}$) and repeated this resampling procedure 1000 times to obtain 1000 values of $\mathrm{MES}_{\mathrm{ran.}}$ We then compared $\mathrm{MES}_{\mathrm{common}}$ to each $\mathrm{MES}_{\mathrm{ran}}$ value to calculate the probability that $\mathrm{MES}_{\mathrm{common}}$ was higher than a random subset of 15 studies taken from the whole data set (Manly, 1997).

We then investigated the variability in effect sizes (*Zr*) and the potential moderators. We analysed the heterogeneity in effect sizes across articles using the I^2 statistic, which was calculated using an intercept model with the article ID as the random effect and se_{Zr} as the weighting parameter (Higgins & Thompson, 2002; Senior *et al.*, 2016). Finally, we tested whether effect sizes (*Zr*) differed among organism types with intraspecific variation manipulation, and among the ecological response variables considered. We hence computed meta-regressions based on linear mixed-effect models with *Zr* values (for all 75 studies and 502 measures) as the dependent variable, and organism type or ecological response variable as fixed effects. The article ID was included as a random effect, and se_{Zr} was included as a weighting parameter. Four models were run to assess the differences of effect sizes (i) between organism types classified as consumers or primary producers, and (ii) between detailed taxonomic categories (arthropods, fishes, herbaceous plants and trees). We then tested whether the effect sizes of intraspecific variation differed among ecological response variables (iii) classified as community or ecosystem variables, and (iv) classified according to more detailed categories (abundance, biomass, community structure, decomposition, nutrient cycling, primary productivity and respiration of the ecosystem).

Publication bias

For both intraspecific variation and intraspecific richness, we assessed potential publication bias by combining Egger's regressions and funnel plots (Egger *et al.*, 1997). Egger's regressions and funnel plots were computed using the residuals of meta-regressions related effect sizes to the main modifiers (i.e. the explanatory variables) and a measure of study size (the inverse of se_{Zr} and sample size for intraspecific variation and intraspecific richness, respectively; Horvathova, Nakagawa & Uller, 2012; Nakagawa & Santos, 2012). Typically, for intraspecific variation we ran an Egger's regression model including the residuals of the meta-regression linking intraspecific variation to the modifiers as a response variable and the inverse of se_{Zr} as the explanatory variable. A similar approach was used for intraspecific richness. The intercept α and the slope β of the Egger's regressions are expected not to differ significantly from zero if the data sets are not biased towards significant results. Finally, funnel plots were produced as a scatterplot linking the residuals described above to the respective measure of the study size. An unbiased data set is expected to generate a funnel plot in which articles with larger sample sizes will be close to the mean effect size, whereas articles with small sample sizes will show more variance around the mean effect size (Horvathova *et al.*, 2012; Nakagawa & Santos, 2012).

Overall, and after accounting for important modifiers we found that there was no strong visual sign of publication bias, neither for intraspecific variation nor for intraspecific richness (Figure III.S2). This visual inspection of funnel plots was confirmed by the Egger's regressions since parameter values were not significant for intraspecific variation ($\alpha = 0.015$, $P = 0.404$; $\beta = -0.001$, $P = 0.501$) or for intraspecific richness ($\alpha = -0.001$, $P = 0.914$; $\beta < 0.001$, $P = 0.961$).

All statistical analyses were performed using the R environment (R core team, 2013). The nlme package (Pinheiro *et al.*, 2014) was used to compute linear and non-linear mixed-effect models, unless specified otherwise.

Results

All articles ($N = 90$) selected for investigating the effects of intraspecific richness and intraspecific variation were published between 2000 and 2018, and 74% used primary producers as target species (Figure III.1). The first studies focusing on consumers were published in 2008, using fish (60%), arthropods (32%), and fungi (8%) as model species.

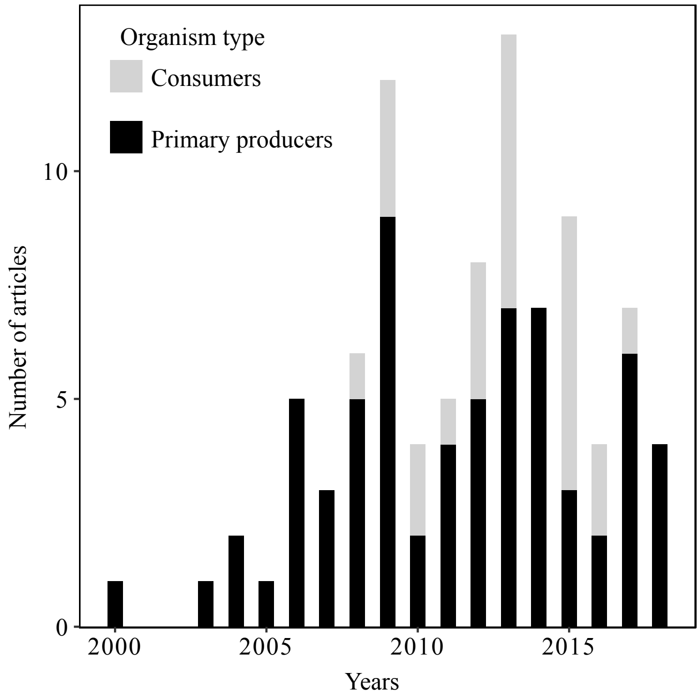


Figure III.1. Publication year of the 90 selected articles used in the meta-analysis.

The intraspecific richness-ecological dynamics relationship

As expected, we found a significant, positive and non-linear relationship between intraspecific richness and ecological dynamics that approximated a saturating curve (Figure III.2a). The AIC selection procedure revealed that one out of the four tested models was highly likely to be supported by the data (i.e. 99% chance of being the best fitting model according to the Akaike weight and ΔAIC > 15.721 for the other models, Table III.1). The model that best supported the data was the exponential asymptotic model, suggesting that the relationship between intraspecific richness and changes in community structure and ecosystem functioning (i.e. effect size: ln*RR*) likely followed a saturating shape (Figure III.2a).

Table III.1. Summary table of model selection by Akaike information criterion (AIC) comparison to explain the shape of the relationship between the ecological consequences and the intraspecific richness. Models were run as non-linear mixed-effect models with the article ID as a random factor; equations and parameters estimates are also shown. IR, intraspecific richness; lnRR, effect size of intraspecific richness on ecological dynamics.

Model	AIC	ΔAIC	AIC weight	Equation	Parameter estimates
Asymptotic exponential model	–176.695	0	0.999	$lnRR = a * (1 - e^{-b*IR})$	$a = 0.221$ $b = 0.617$
Michaelis–Menten model	–11.873	164.821	< 0.001	$lnRR = V * \frac{IR}{k + IR}$	$V = 0.054$ $k = -2.712$
Linear model	–160.974	15.721	< 0.001	$lnRR = b0 + b1 * IR$	$b1 = 0.012$ $b0 = 0.122$
Null model	–144.191	32.503	< 0.001	$lnRR = b0$	$b0 = 0.183$

We further found that the ecological effects of intraspecific richness were similar to the ecological effects induced by interspecific richness (Figure III.2b). Indeed, the two distributions largely overlapped and the estimated means were similar (intraspecific richness |lnRR| = 0.132, PI = 0.048–0.216; interspecific richness |lnRR| = 0.134 PI = 0.012–0.462). The ecological effects of intraspecific richness tended to be higher, although the difference was not significant, for community metrics (|lnRR| = 0.156, PI = 0.070–0.242) than for ecosystem metrics (|lnRR| = 0.045, PI = 0.004–0.137) (see Figure III.S3 for details of ecological metrics).

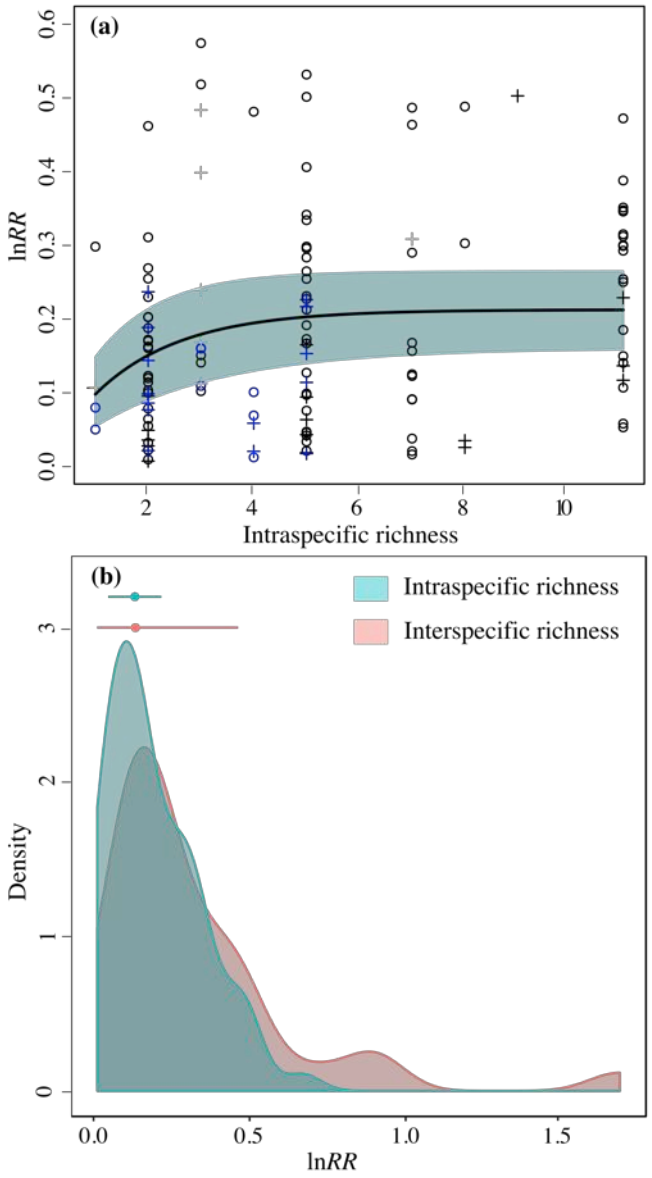


Figure III.2. (a) Relationship between intraspecific richness and effect size (ln*RR*) on community (points) and ecosystem (crosses) dynamics. The line represents the shape of the relationship as predicted using an exponential asymptotic non-linear mixed effect model. The blue shadow represents 95% CI. Symbol colours denote the target species: herbaceous plant (black), tree (blue) or fungus (grey). **(b)** Density of absolute effect size (ln*RR*) for intraspecific and interspecific richness on ecological dynamics. Posterior means and 95% percentile intervals (points and horizontal lines, respectively) were estimated using a model including article ID as the random effect and the inverse of sample size as a weighting parameter.

The ecological consequences of intraspecific variation

We extended the meta-analysis performed by Des Roches *et al.* (2018) to 51 species (15 species were used in Des Roches *et al.*, 2018). We found that the observed effect size of intraspecific variation on community structure and ecosystem dynamics was significant, and was twice as large as the resampled effect size expected under the null expectation ($\mathrm{MES}_{\mathrm{obs}}$ = 0.521, 95% confidence interval (CI) = 0.444–0.598; $\mathrm{MES}_{\mathrm{null}}$ = 0.259, CI = 0.258–0.259; resampled test, $P < 0.001$; see Figures III.3 and III.S4).

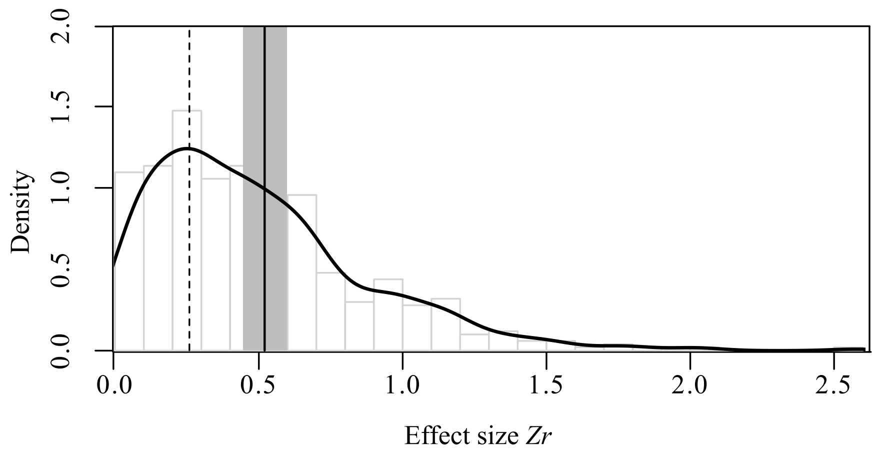


Figure III.3. Density probability of effect size *Zr*. The vertical broken line represents the resampled *Zr* mean under the null hypothesis (confidence intervals not shown because they are too narrow); the black curve shows the distribution of observed *Zr* and its mean (vertical black straight line) and 95% CIs (grey shading).

We tested the extent to which the more restricted data set of Des Roches *et al.* (2018) was representative of our extended data set, or whether it was upwardly biased as expected by Des Roches *et al.* (2018). We found that effect sizes for studies in common with the Des Roches *et al.* (2018) data set (MES_{common} = 0.299, 95% percentile interval (PI) = 0.033–1.092) were not significantly different from the distribution of effect sizes measured in our extended data set (MES_{ran} = 0.418, PI = 0.255–0.616; resampling test, $P = 0.118$; Figure III.S5), and in fact showed a tendency to be downwardly biased.

Finally, a relatively low heterogeneity in effect size (*Zr*) was detected across articles ($I^2 = 0.151$). The ecological effects induced by intraspecific variation were stronger when primary producers rather than consumers were manipulated ($F = 3.968$ d.f. = 1, 425, $P =$ 0.047; Figure III.4a). Nonetheless, the strongest ecological effects of intraspecific variation tended to be observed in arthropods and herbaceous species, whereas the smallest effects were observed in fish and tree species ($F = 2.475$ d.f. = 3, 417, $P = 0.061$; Figure III.4a). Irrespective of organism type, the effects of intraspecific variation were significantly stronger when the response variables were measured at the ecosystem level rather than at the community level ($F = 7.295$, d.f = 1, 425, $P = 0.007$; Figure III.4b). The strongest effects were detected when response variables concerned nutrient cycling and the assembly of community, whereas the lowest effects were found for general measures of abundance and density of species ($F = 2.725$, d.f = 6, 417, $P = 0.013$; Figure III.4b).

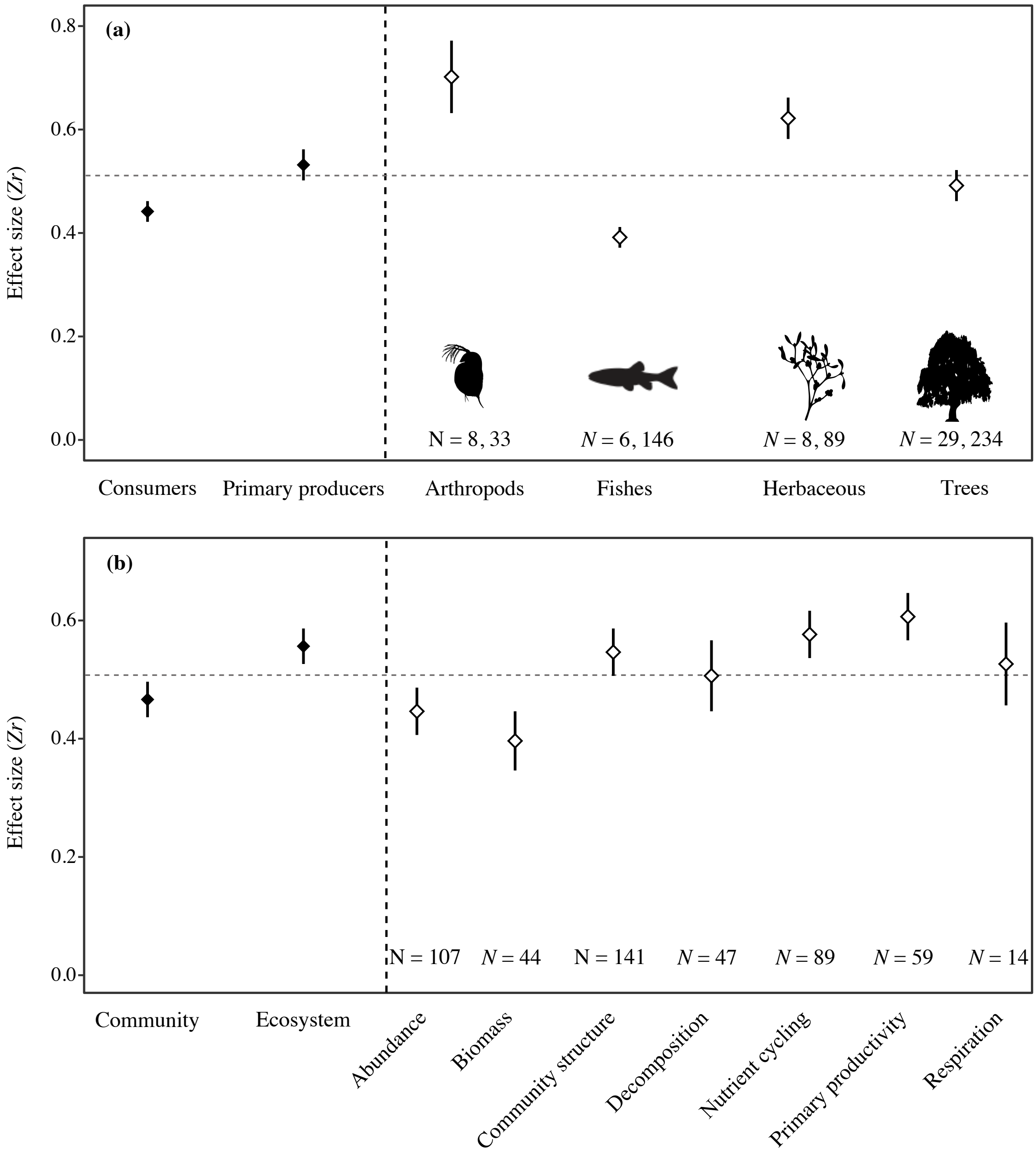


Figure III.4. (a) Mean effect size *Zr* for different species groups. The sample sizes (*N*) represent the number of species and the number of effect sizes, respectively. The horizontal broken line represents the mean effect size; error bars represent ± 1 SE. **(b)** Mean *Zr* for the ecological response variables. The sample sizes (*N*) of the number of effect sizes are given. The horizontal broken line represents the mean effect size; error bars represent ± 1 SE.

Discussion

Intraspecific diversity is increasingly recognized as an important facet of biodiversity that can affect all biological levels (Bailey *et al.*, 2009). Several studies have experimentally tested the ecological effects of intraspecific diversity, and we here provide the first global and quantitative estimates of the consequences of intraspecific richness and variation on community structure and ecosystem functioning. We demonstrated for the first time that the intraspecific BEF followed – as theoretically expected – a non-linear saturating curve with a plateau at 4–6 genotypes per population. Importantly, we demonstrated also for the first time that intraspecific richness affects community and ecosystem dynamics with a magnitude comparable to that of biodiversity measured at the species level. We further confirmed and extended the result that genotypic and/or phenotypic variation observed between populations can have non-negligible effects on community structure and ecosystem functions, and we demonstrated that previous estimates (Des Roches *et al.*, 2018) of these ecological effects of intraspecific variation actually tended to be underestimated. Finally, our exhaustive quantitative survey identified that the ecological consequences of intraspecific variation differ among biological level of organization, and among organism types. These findings provide novel and integrative insights, as well as multiple research perspectives, into the ecological role of intraspecific diversity.

Intraspecific diversity and the dynamics of communities and ecosystems

Although the form of the relationship between intraspecific richness and ecological consequences has already been discussed conceptually (Hughes *et al.*, 2008), our meta-analysis provides for the first time a qualitative and quantitative assessment of intraspecific BEF measured experimentally. Specifically, although considering mostly primary producers, our results demonstrated that an increase in intraspecific richness resulted in a non-linear (saturating) increase in the magnitude of its effects on ecological dynamics. This finding supports the idea that ecological divergence between an environment hosting populations composed of a single genotype and an environment hosting populations composed of multiple genotypes increases until a plateau is reached as the number of genotypes increases. This result echoes the BEF as defined at the interspecific level (Reiss *et al.*, 2009; Cadotte, Carscadden & Mirotchnick, 2011) and suggests that the saturating shape might arise from similar mechanisms occurring at the intraspecific and interspecific levels (Johnson *et al.*, 2006; Hughes *et al.*, 2008). More specifically, the initial linear increase is assumed to be due to complementarity and facilitation among genotypes, whereas the plateau likely occurs due to functional redundancy among genotypes (Johnson *et al.*, 2006). Redundant genotypes probably display functionally similar traits since two genotypes do not necessarily generate two functionally different traits (e.g. through synonymous mutations or trait convergences). Thus manipulating trait richness rather than genotypic richness, or more precisely manipulating functional effect traits [i.e. traits with ecological effects (Violle *et al.*, 2007)], in future experiments should allow us to explore the mechanisms underlying the intraspecific biodiversity–ecological dynamics relationship.

We found that effect sizes for intraspecific richness were very similar to values reported recently reported for experimental interspecific BEF, indicating that the ecological effects of varying phenotypic/genotypic richness within populations are close to those induced by varying species richness within communities. This finding raises several questions regarding the general relationships among intraspecific diversity, community structure, ecosystem functioning and common abiotic constraints. A large body of literature has demonstrated that intraspecific genetic diversity and species diversity (a measure of community structure) might co-vary because of common environmental drivers and/or reciprocal causal relationships between intraspecific genetic diversity and species diversity [i.e. the species–genetic diversity correlation (SGDC) framework (Vellend & Geber, 2005; Vellend, 2005)]. Because most studies considered in our meta-analysis are experimental, our findings confirm that intraspecific diversity can directly influence the structure of communities irrespective of the abiotic environments, hence adding weight to the SGDC framework. Additionally, we suggest expanding the SGDC framework since intraspecific diversity can also affect ecosystem functioning. This suggests that intraspecific diversity, community structure and ecosystem functioning may actually be tightly linked in a tripartite relationship. A major future challenge will be to tease apart the causal relationships linking these three components within a common abiotic environment. These relationships might be direct (e.g. intraspecific diversity directly affects community structure), indirect (e.g. intraspecific diversity indirectly affects ecosystem functions through its direct effect on community structure such as the trophic cascade), and/or due to the parallel effects of common abiotic drivers (e.g. temperature directly affects intraspecific diversity, community structure and ecosystem functions). As has been done recently for the BEF (Grace *et al.*, 2016; Duffy *et al.*, 2016) and the SGDC (Fourtune *et al.*, 2016; Lamy *et al.*, 2017) frameworks, we argue that a future important step will be to combine powerful statistical methods (e.g. path analysis; Shipley, 2000; Grace, 2006) with appropriate experimental designs to disentangle causal relationships between intraspecific diversity, community structure, ecosystem functions and their common environment.

We further demonstrated that intraspecific variation has significant ecological effects across a large set of species (51 species and 75 articles), hence confirming and refining a previous estimate based on a more restricted species set (Des Roches *et al.*, 2018). By more than tripling the number of species being investigated in this meta-analysis, we extend the conclusion to a greater taxonomic set that intraspecific variation is involved in shaping ecological dynamics, and that the ecological effects of intraspecific variation might be more common than expected. Moreover, we demonstrated that previous estimates (Des Roches *et al.*, 2018) were not upwardly biased (as expected from their focus on a non-random species pool), but were well within the range of estimates we report here and actually tended to be slight underestimates. Our finding hence strongly supports the idea that adaptive and non-adaptive processes can lead to unique populations differentially and significantly affecting ecological systems.

Although our conclusions held true for many species, the ecological effects of intraspecific variation were not homogeneous across species, and this was partly explained by their trophic level. Indeed, and according to expectations, the ecological effects of intraspecific variation were stronger when the target species was a primary producer than when it was a consumer. Several non-exclusive mechanisms might explain this result. For instance, many primary producers considered here provide a habitat for many invertebrate species (Southwood, Brown & Reader, 1979) (this is not the case for the consumer species), and this habitat can be modulated by changes in plant structure. The relative biomass of primary producers is higher than that of consumers, thus primary producers could generate stronger effects on communities and ecosystems than consumers simply because of this biomass effect. However, a more detailed analysis showed that the effects of intraspecific variation tended to be stronger for arthropod and herbaceous species than for fish (and to a lesser extent tree) species. This suggests that the trophic level of a species may not be the only predictor of the ecological effects of intraspecific diversity, and we argue that future work should aim to test specifically why intraspecific variation matters more for some species than others.

Finally, the effects of intraspecific variation were globally higher for ecosystems than for communities, hence generalizing across organism and ecosystem types a previous conclusion for freshwater consumer species (Palkovacs *et al.*, 2015). We can speculate that this difference arises because intraspecific variation acts on community dynamics through trophic mechanisms, whereas ecosystem functions can be modulated through both trophic and non-trophic interactions [e.g. excretion rate or leaf chemistry (Vanni, 2002; Schmitz *et al.*, 2014)]. For instance, a consumer species that shows intraspecific variation in resource selectivity and/or consumption rate could affect both the community structure and productivity of its resource (Harmon *et al.*, 2009). Non-trophic mechanisms such as variability in organismal stoichiometry could reinforce the effect of the consumer species on several ecosystem functions [e.g. primary production or soil mineralization (Schmitz, Hawlena & Trussell, 2010; Hawlena *et al.*, 2012)]. Alternatively, changes in ecosystem functions might be due to both direct effects of intraspecific diversity and indirect effects of intraspecific diversity mediated through changes in community structure, which may overall strengthen the effects of intraspecific diversity at the ecosystem level. However, a more detailed analysis revealed that much variation exists between sub-categories of response variables (Figure III.4b), and that the dichotomy between variables measured at the community and ecosystem levels is not straightforward. Although providing the first attempts to separate variance in the ecological effects of intraspecific variation into its component parts, our findings call for further studies on various taxa and in different ecosystems in order to understand fully the ecological effects of intraspecific diversity.

Research perspectives on the relationships between intraspecific diversity and the dynamics of communities and ecosystems

We highlight several research avenues that may greatly enhance our understanding of the relationships between intraspecific diversity and the dynamics of communities and ecosystems.

Our review demonstrates that the ecological effect size of intraspecific diversity varies among species and that this interspecific variance in effect size can be partly explained by the type of organism (i.e. primary producer or consumer). However, species composing a community also vary according to abundance, role in the ecosystem (e.g. keystone species; Paine, 1969), body size (or height for plants), life-history strategy (e.g. *r*–*K* strategy), recent history (e.g. whether the species is non-native), functional characteristics (e.g. stoichiometry, metabolism), etc. The next challenge will be to partition this interspecific variance in effect size better by determining the species characteristics that best predict the strength of effect sizes; this is a pre-requisite to design coherent conservation plans at the intraspecific level (Mimura *et al.*, 2016).

Intraspecific diversity is often manipulated with respect to a single target species. However, in nature, species are interacting and we argue that future studies should manipulate intraspecific diversity within multiple interacting species to reflect natural conditions, and to allow partitioning the relative importance of intraspecific diversity between interacting (and potentially co-evolving) species.

Ecosystems are interconnected through cross-ecosystem fluxes of matter (Loreau, Mouquet & Holt, 2003). For instance, freshwater ecosystems such as rivers receive a large amount of material from surrounding terrestrial ecosystems [e.g. dead leaves falling from trees (Bartels *et al.*, 2012)]. A major future challenge would be to assess the relative effects of intraspecific diversity on allochtonous ecosystems *versus* autochtonous ecosystems; for example testing whether the consequences of intraspecific diversity manipulation in a fish species are greater in associated aquatic ecosystems than on nearby terrestrial ecosystems [see Jackrel & Wootton (2014), Crutsinger *et al.* (2014)*b* and Rudman *et al.* (2015) for attempts to quantify across-ecosystem effects of intraspecific diversity]. This is an important next step to quantify in a more integrative way the importance of intraspecific diversity in natural systems.

Previous studies have mainly assessed the consequences of intraspecific diversity by considering the genetic or the phenotypic characteristics of organisms as a whole. However, some traits have been shown to be more important for ecological dynamics than others; this is the case for functional effect traits that are defined as traits with an ecological impact [e.g. excretion rate or leaf nutrient content (Violle *et al.*, 2007; Díaz *et al.*, 2013)]. We suggest that direct manipulation of the functional trait diversity of individuals within a species, rather than their genotypic or phenotypic diversity as a whole would be a powerful means to understanding the mechanisms by which intraspecific diversity acts on ecological dynamics.

Although we emphasize that intraspecific diversity is an essential component of the community and ecosystem facets of ecological dynamics, comparisons with the effects of other major ecological constraints (e.g. temperature, interspecific biodiversity, human disturbance) have rarely been conducted (but see Burkle *et al.*, 2013; El-Sabaawi *et al.*, 2015). To evaluate and quantify the importance of intraspecific diversity in natural systems better, it is important to assess the relative contributions of intraspecific diversity and other determinants of ecosystem functioning. This will be an essential step in confirming that intraspecific variation is a key determinant, and not just a random signal in complex systems.

Conclusions

(1) This study provides empirical evidence that the ecological effects of intraspecific richness increase asymptotically, paralleling well-known patterns observed at the interspecific level

(Loreau, 2000; Hooper *et al.*, 2005) and confirming previous hypotheses (Hughes *et al.*, 2008).

(2) We found that experimental manipulations of intraspecific richness caused community and ecosystem differentiations as large as those generated by interspecific richness. This suggests that variation in richness within populations can have similar ecological consequences to variation in richness among species.

(3) We also demonstrated that variation in phenotypes or genotypes within species is an important driver of community and ecosystem dynamics. These major ecological effects of intraspecific diversity held true for a range of organisms including plants and animals, although much remains to be tested.

(4) Overall these findings demonstrate that intraspecific diversity - beyond its importance for species to adapt to environmental changes - is an important facet of biodiversity for understanding and predicting the ecological dynamics of communities and ecosystems, reinforcing the need for a better appraisal of the causes and consequences of intraspecific diversity in natural populations and for improved conservation plans.

Acknowledgements

We warmly thank José M. Montoya for valuable comments on a previous version of this review. We also thank three anonymous reviewers for their constructive and useful comments. A.R. was supported financially by a Doctoral scholarship from the Université Fédérale de Toulouse. This work was undertaken at SETE, which is part of the "Laboratoire d'Excellence" (LABEX) entitled TULIP (ANR-10-LABX-41).

References

ABBOTT, J.M., GROSBERG, R.K., WILLIAMS, S.L. & STACHOWICZ, J.J. (2017). Multiple dimensions of intraspecific diversity affect biomass of eelgrass and its associated community. *Ecology* **98**, 3152–3164.

BAILEY, J.K., SCHWEITZER, J.A., UBEDA, F., KORICHEVA, J., LEROY, C.J., MADRITCH, M.D., REHILL, B.J., BANGERT, R.K., FISCHER, D.G., ALLAN, G.J. & WHITHAM, T.G. (2009). From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1607–1616.

BARBOUR, M.A., FORTUNA, M.A., BASCOMPTE, J., NICHOLSON, J.R., JULKUNEN-TIITTO, R., JULES, E.S. & CRUTSINGER, G.M. (2016). Genetic specificity of a plant–insect food web:

Implications for linking genetic variation to network complexity. *Proceedings of the National Academy of Sciences* **113**, 2128–2133.

BARBOUR, R.C., FORSTER, L.G., BAKER, S.C., STEANE, D.A. & POTTS, B.M. (2009*a*). Biodiversity consequences of genetic variation in bark characteristics within a foundation tree species. *Conservation Biology* **23**, 1146–1155.

BARBOUR, R.C., O'REILLY-WAPSTRA, J.M., DE LITTLE, D.W., JORDAN, G.J., STEANE, D.A., HUMPHREYS, J.R., BAILEY, J.K., WHITHAM, T.G. & POTTS, B.M. (2009*b*). A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology* **90**, 1762–1772.

BARBOUR, R.C., STORER, M.J. & POTTS, B.M. (2009*c*). Relative importance of tree genetics and microhabitat on macrofungal biodiversity on coarse woody debris. *Oecologia* **160**, 335–342.

BARRIOS-GARCIA, M.N., RODRIGUEZ-CABAL, M.A., RUDGERS, J.A. & CRUTSINGER, G.M. (2016). Soil fertilization does not alter plant architectural effects on arthropod communities. *Journal of Plant Ecology*, rtw087.

BARTELS, P., CUCHEROUSSET, J., STEGER, K., EKLÖV, P., TRANVIK, L.J. & HILLEBRAND, H. (2012). Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* **93**, 1173–1182.

BASSAR, R.D., MARSHALL, M.C., LOPEZ-SEPULCRE, A., ZANDONA, E., AUER, S.K., TRAVIS, J., PRINGLE, C.M., FLECKER, A.S., THOMAS, S.A., FRASER, D.F. & REZNICK, D.N. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences* **107**, 3616–3621.

BOLNICK, D.I., AMARASEKARE, P., ARAÚJO, M.S., BÜRGER, R., LEVINE, J.M., NOVAK, M., RUDOLF, V.H., SCHREIBER, S.J. & URBAN, M.C. (2011). Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution* **26**, 183–192.

BOLNICK, D.I., SVANBÄCK, R., FORDYCE, J.A., YANG, L.H., DAVIS, J.M., HULSEY, C.D. & FORISTER, M.L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**, 1–28.

BOOTH, R.E. & GRIME, J.P. (2003). Effects of genetic impoverishment on plant community diversity. *Journal of Ecology* **91**, 721–730.

BURKLE, L.A., SOUZA, L., GENUNG, M.A. & CRUTSINGER, G.M. (2013). Plant genotype, nutrients, and G X E interactions structure floral visitor communities. *Ecosphere* **4**.

BURNHAM, K.P. & ANDERSON, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach.* Springer, New York.

BUSTOS-SEGURA, C., POELMAN, E.H., REICHELT, M., GERSHENZON, J. & GOLS, R. (2017). Intraspecific chemical diversity among neighbouring plants correlates positively with plant size and herbivore load but negatively with herbivore damage. *Ecology Letters* **20**, 87–97.

CADOTTE, M.W., CARSCADDEN, K. & MIROTCHNICK, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48**, 1079–1087.

CAMPOS-NAVARRETE, M.J., MUNGUÍA-ROSAS, M.A., ABDALA-ROBERTS, L., QUINTO, J. & PARRA-TABLA, V. (2015). Effects of tree genotypic diversity and species diversity on the arthropod community associated with big-leaf mahogany. *Biotropica* **47**, 579–587.

CARDINALE, B.J., DUFFY, J.E., GONZALEZ, A., HOOPER, D.U., PERRINGS, C., VENAIL, P., NARWANI, A., MACE, G.M., TILMAN, D., WARDLE, D.A., KINZIG, A.P., DAILY, G.C., LOREAU, M., GRACE, J.B., LARIGAUDERIE, A., ET AL. (2012). Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67.

CHAPIN, S.F., ZAVALETA, E.S., EVINER, V.T., NAYLOR, R.L., VITOUSEK, P.M., REYNOLDS, H.L., HOOPER, D.U., LAVOREL, S., SALA, O.E., HOBBIE, S.E., MACK, M.C. & DÍAZ, S. (2000). Consequences of changing biodiversity. *Nature* **405**, 234–242.

CHISLOCK, M.F., SARNELLE, O., OLSEN, B.K., DOSTER, E. & WILSON, A.E. (2013). Large effects of consumer offense on ecosystem structure and function. *Ecology* **94**, 2375–2380.

CLASSEN, A.T., CHAPMAN, S.K., WHITHAM, T.G., HART, S.C. & KOCH, G.W. (2007). Genetic-based plant resistance and susceptibility traits to herbivory influence needle and root litter nutrient dynamics. *Journal of Ecology* **95**, 1181–1194.

COOK-PATTON, S.C., MCART, S.H., PARACHNOWITSCH, A.L., THALER, J.S. & AGRAWAL, A.A. (2011). A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. *Ecology* **92**, 915–923.

CORNELISSEN, J.H.C., PEREZ-HARGUINDEGUY, N., GWYNN-JONES, D., DIAZ, S., CALLAGHAN, T.V. & AERTS, R. (2000). Autumn leaf colours as indicators of decomposition rate in sycamore (*Acer pseudoplatanus L.*). *Plant and Soil* **225**, 33–38.

CRAWFORD, K.M. & RUDGERS, J.A. (2013). Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology* **94**, 1025–1035.

CRUTSINGER, G.M., CADOTTE, M.W. & SANDERS, N.J. (2009*a*). Plant genetics shapes inquiline community structure across spatial scales. *Ecology Letters* **12**, 285–292.

CRUTSINGER, G.M., CARTER, B.E. & RUDGERS, J.A. (2013). Soil nutrients trump intraspecific effects on understory plant communities. *Oecologia* **173**, 1531–1538.

CRUTSINGER, G.M., COLLINS, M.D., FORDYCE, J.A., GOMPERT, Z., NICE, C.C. & SANDERS, N.J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* **313**, 966–968.

CRUTSINGER, G.M., COLLINS, M.D., FORDYCE, J.A. & SANDERS, N.J. (2008*a*). Temporal dynamics in non-additive responses of arthropods to host-plant genotypic diversity. *Oikos* **117**, 255–264.

CRUTSINGER, G.M., REYNOLDS, W.N., CLASSEN, A.T. & SANDERS, N.J. (2008*b*). Disparate effects of plant genotypic diversity on foliage and litter arthropod communities. *Oecologia* **158**, 65–75.

CRUTSINGER, G.M., RODRIGUEZ-CABAL, M.A., RODDY, A.B., PEAY, K.G., BASTOW, J.L., KIDDER, A.G., DAWSON, T.E., FINE, P.V.A. & RUDGERS, J.A. (2014*a*). Genetic variation within a dominant shrub structures green and brown community assemblages. *Ecology* **95**, 387–398.

CRUTSINGER, G.M., RUDMAN, S.M., RODRIGUEZ-CABAL, M.A., MCKOWN, A.D., SATO, T., MACDONALD, A.M., HEAVYSIDE, J., GERALDES, A., HART, E.M., LEROY, C.J. & EL-SABAAWI, R.W. (2014*b*). Testing a 'genes-to-ecosystems' approach to understanding aquatic-terrestrial linkages. *Molecular Ecology* **23**, 5888–5903.

CRUTSINGER, G.M., SANDERS, N.J. & CLASSEN, A.T. (2009*b*). Comparing intra- and inter-specific effects on litter decomposition in an old-field ecosystem. *Basic and Applied Ecology* **10**, 535–543.

DE BELLO, F., LAVOREL, S., ALBERT, C.H., THUILLER, W., GRIGULIS, K., DOLEZAL, J., JANECEK, S. & LEPS, J. (2011). Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution* **2**, 163–174.

DE GRAAFF, M.-A., SIX, J., JASTROW, J.D., SCHADT, C.W. & WULLSCHLEGER, S.D. (2013). Variation in root architecture among switchgrass cultivars impacts root decomposition rates. *Soil Biology & Biochemistry* **58**, 198–206.

DES ROCHES, S., POST, D.M., TURLEY, N.E., BAILEY, J.K., HENDRY, A.P., KINNISON, M.T., SCHWEITZER, J.A. & PALKOVACS, E.P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution* **2**, 57–64.

DES ROCHES, S., SHURIN, J.B., SCHLUTER, D. & HARMON, L.J. (2013). Ecological and evolutionary effects of stickleback on community structure. *PLoS ONE* **8**, e59644.

DÍAZ, S., PURVIS, A., CORNELISSEN, J.H.C., MACE, G.M., DONOGHUE, M.J., EWERS, R.M., JORDANO, P. & PEARSE, W.D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3**, 2958–2975.

DOWNING, A.L. & LEIBOLD, M.A. (2002). Ecosystem consequences of species richness and composition in pond food web. *Nature* **416**, 837–-841.

DUFFY, J.E., GODWIN, C.M. & CARDINALE, B.J. (2017). Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* **549**, 261–264.

DUFFY, J.E., LEFCHECK, J.S., STUART-SMITH, R.D., NAVARRETE, S.A. & EDGAR, G.J. (2016). Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences* **113**, 6230–6235.

EGGER, M., SMITH, G.D., SCHNEIDER, M. & MINDER, C. (1997). Bias in meta-analysis detected by a simple graphical test. *Bmj* **315**, 629–634.

EL-SABAAWI, R.W., BASSAR, R.D., RAKOWSKI, C., MARSHALL, M.C., BRYAN, B.L., THOMAS, S.N., PRINGLE, C., REZNICK, D.N. & FLECKER, A.S. (2015). Intraspecific phenotypic differences in fish affect ecosystem processes as much as bottom-up factors. *Oikos* **124**, 1181–1191.

FARKAS, T.E., MONONEN, T., COMEAULT, A.A., HANSKI, I. & NOSIL, P. (2013). Evolution of camouflage drives rapid ecological change in an insect community. *Current Biology* **23**, 1835–1843.

FOURTUNE, L., PAZ-VINAS, I., LOOT, G., PRUNIER, J.G. & BLANCHET, S. (2016). Lessons from the fish: a multi-species analysis reveals common processes underlying similar species-genetic diversity correlations. *Freshwater Biology* **61**, 1830–1845.

FRIDLEY, J.D. & GRIME, J.P. (2010). Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology* **91**, 2272–2283.

FRYXELL, D.C., ARNETT, H.A., APGAR, T.M., KINNISON, M.T. & PALKOVACS, E.P. (2015). Sex ratio variation shapes the ecological effects of a globally introduced freshwater fish. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20151970.

GENUNG, M.A., LESSARD, J.-P., BROWN, C.B., BUNN, W.A., CREGGER, M.A., REYNOLDS, W.N., FELKER-QUINN, E., STEVENSON, M.L., HARTLEY, A.S., CRUTSINGER, G.M., SCHWEITZER, J.A. & BAILEY, J.K. (2010). Non-additive effects of genotypic diversity increase floral abundance and abundance of floral visitors. *Plos One* **5**, e8711.

GOITOM, E., KILSDONK, L.J., BRANS, K., JANSEN, M., LEMMENS, P. & DE MEESTER, L. (2018). Rapid evolution leads to differential population dynamics and top-down control in resurrected *Daphnia* populations. *Evolutionary Applications* **11**, 96–111.

GRACE, J.B. (2006). *Structural equation modeling and natural systems.* Cambridge University Press.

GRACE, J.B., ANDERSON, T.M., SEABLOOM, E.W., BORER, E.T., ADLER, P.B., HARPOLE, W.S., HAUTIER, Y., HILLEBRAND, H., LIND, E.M., PÄRTEL, M., BAKKER, J.D., BUCKLEY, Y.M., CRAWLEY, M.J., DAMSCHEN, E.I., DAVIES, K.F., ET AL. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* **529**, 390–393.

GRANT, P.R. & GRANT, B.R. (2006). Evolution of character displacement in darwin's finches. *Science* **313**, 224–226.

HADFIELD, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1–22.

HARMON, L.J., MATTHEWS, B., DES ROCHES, S., CHASE, J.M., SHURIN, J.B. & SCHLUTER, D. (2009). Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* **458**, 1167–1170.

HARRISON, J.G., PHILBIN, C.S., GOMPERT, Z., FORISTER, G.W., HERNANDEZ-ESPINOZA, L., SULLIVAN, B.W., WALLACE, I.S., BELTRAN, L., DODSON, C.D., FRANCIS, J.S., SCHLAGETER, A., SHELEF, O., YOON, S.A. & FORISTER, M.L. (2018). Deconstruction of a plant-arthropod community reveals influential plant traits with nonlinear effects on arthropod assemblages. *Functional Ecology* **32**, 1317–1328.

HAWLENA, D., STRICKLAND, M.S., BRADFORD, M.A. & SCHMITZ, O.J. (2012). Fear of predation slows plant-litter decomposition. *Science* **336**, 1434–1438.

HIGGINS, J.P.T. & THOMPSON, S.G. (2002). Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine* **21**, 1539–1558.

HILLEBRAND, H. & MATTHIESSEN, B. (2009). Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters* **12**, 1405–1419.

HINES, J., REYES, M., MOZDER, T.J. & GESSNER, M.O. (2014). Genotypic trait variation modifies effects of climate warming and nitrogen deposition on litter mass loss and microbial respiration. *Global Change Biology* **20**, 3780–3789.

HOOPER, D.U., CHAPIN, F.S., EWEL, J.J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J.H., LODGE, D.M., LOREAU, M., NAEEM, S., SCHMID, B., SETÄLÄ, H., SYMSTAD, A.J., VANDERMEER, J. & WARDLE, D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.

HORVATHOVA, T., NAKAGAWA, S. & ULLER, T. (2012). Strategic female reproductive investment in response to male attractiveness in birds. *Proceedings of the Royal Society B: Biological Sciences* **279**, 163–170.

HOWETH, J.G., WEIS, J.J., BRODERSEN, J., HATTON, E.C. & POST, D.M. (2013). Intraspecific phenotypic variation in a fish predator affects multitrophic lake metacommunity structure. *Ecology and Evolution* **3**, 5031–5044.

HUANG, J., LIU, M., CHEN, X., CHEN, J., LI, H. & HU, F. (2015). Effects of intraspecific variation in rice resistance to aboveground herbivore, brown planthopper, and rice root nematodes on plant yield, labile pools of plant, and rhizosphere soil. *Biology and Fertility of Soils* **51**, 417–425.

HUGHES, A.R. (2014). Genotypic diversity and trait variance interact to affect marsh plant performance. *Journal of Ecology* **102**, 651–658.

HUGHES, A.R., INOUYE, B.D., JOHNSON, M.T.J., UNDERWOOD, N. & VELLEND, M. (2008). Ecological consequences of genetic diversity. *Ecology Letters* **11**, 609–623.

INGRAM, T., SVANBÄCK, R., KRAFT, N.J.B., KRATINA, P., SOUTHCOTT, L. & SCHLUTER, D. (2012). Intraguild predation drives evolutionary niche shift in threespine stickleback. *Evolution* **66**, 1819–1832.

ITO, M. & OZAKI, K. (2005). Response of a gall wasp community to genetic variation in the host plant *Quercus crispula*: a test using half-sib families. *Acta Oecologica* **27**, 17–24.

JACKREL, S.L. & WOOTTON, J.T. (2014). Local adaptation of stream communities to intraspecific variation in a terrestrial ecosystem subsidy. *Ecology* **95**, 37–43.

JOHNSON, M.T. & AGRAWAL, A.A. (2005). Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology* **86**, 874–885.

JOHNSON, M.T.J., LAJEUNESSE, M.J. & AGRAWAL, A.A. (2006). Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* **9**, 24–34.

JOHNSON, M.T.J., VELLEND, M. & STINCHCOMBE, J.R. (2009). Evolution in plant populations as a driver of ecological changes in arthropod communities. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1593–1605.

KAGIYA, S., YASUGI, M., KUDOH, H., NAGANO, A.J. & UTSUMI, S. (2018). Does genomic variation in a foundation species predict arthropod community structure in a riparian forest? *Molecular Ecology* **27**, 1284–1295.

KANAGA, M.K., LATTA, L.C., MOCK, K.E., RYEL, R.J., LINDROTH, R.L. & PFRENDER, M.E. (2009). Plant genotypic diversity and environmental stress interact to negatively affect arthropod community diversity. *Arthropod-Plant Interactions* **3**, 249–258.

KATANO, O. (2011). Effects of individual differences in foraging of pale chub on algal biomass through trophic cascades. *Environmental Biology of Fishes* **92**, 101–112.

KORICHEVA, J., GUREVITCH, J. & MENGERSEN, K. (2013). *Handbook of meta-Analysis in ecology and evolution.* Princeton University press, Princeton, New Jersey.

KOTOWSKA, A.M., CAHILL JR, J.F. & KEDDIE, B.A. (2010). Plant genetic diversity yields increased plant productivity and herbivore performance. *Journal of Ecology* **98**, 237–245.

LAGERSTROM, A., NILSSON, M.-C. & WARDLE, D.A. (2013). Decoupled responses of tree and shrub leaf and litter trait values to ecosystem retrogression across an island area gradient. *Plant and Soil* **367**, 183–197.

LAMY, T., LAROCHE, F., DAVID, P., MASSOL, F. & JARNE, P. (2017). The contribution of species-genetic diversity correlations to the understanding of community assembly rules. *Oikos* **126**, 759–771.

LECERF, A. & CHAUVET, E. (2008). Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology* **9**, 598–605.

LEROY, C.J., WHITHAM, T.G., WOOLEY, S.C. & MARKS, J.C. (2007). Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river. *Journal of the North American Benthological Society* **26**, 426–438.

LOREAU, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**, 3–17.

LOREAU, M., MOUQUET, N. & HOLT, R.D. (2003). Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* **6**, 673–679.

LOWE, W.H., KOVACH, R.P. & ALLENDORF, F.W. (2017). Population genetics and demography unite ecology and evolution. *Trends in Ecology & Evolution* **32**, 141–152.

MADRITCH, M., DONALDSON, J.R. & LINDROTH, R.L. (2006). Genetic identity of *Populus tremuloides* litter influences decomposition and nutrient release in a mixed forest stand. *Ecosystems* **9**, 528–537.

MADRITCH, M.D., GREENE, S.L. & LINDROTH, R.L. (2009). Genetic mosaics of ecosystem functioning across aspen-dominated landscapes. *Oecologia* **160**, 119–127.

MADRITCH, M.D. & HUNTER, M.D. (2003). Intraspecific litter diversity and nitrogen deposition affect nutrient dynamics and soil respiration. *Oecologia* **136**, 124–128.

MADRITCH, M.D. & HUNTER, M.D. (2004). Phenotypic diversity and litter chemistry affect nutrient dynamics during litter decomposition in a two species mix. *Oikos* **105**, 125–131.

MADRITCH, M.D. & HUNTER, M.D. (2005). Phenotypic variation in oak litter influences short- and long-term nutrient cycling through litter chemistry. *Soil Biology & Biochemistry* **37**, 319–327.

MADRITCH, M.D. & LINDROTH, R.L. (2011). Soil microbial communities adapt to genetic variation in leaf litter inputs. *Oikos* **120**, 1696–1704.

MANLY, B.F. (1997). *Randomization, bootstrap and Monte Carlo methods in biology.* Chapman and Hall, London.

MATTHEWS, B., AEBISCHER, T., SULLAM, K.E., LUNDSGAARD-HANSEN, B. & SEEHAUSEN, O. (2016). Experimental evidence of an eco-evolutionary feedback during adaptive divergence. *Current Biology* **26**, 483–489.

MATTHEWS, B., DE MEESTER, L., JONES, C.G., IBELINGS, B.W., BOUMA, T.J., NUUTINEN, V., DE KOPPEL, J. VAN & ODLING-SMEE, J. (2014). Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs* **84**, 245–263.

MATTHEWS, B., NARWANI, A., HAUSCH, S., NONAKA, E., PETER, H., YAMAMICHI, M., SULLAM, K.E., BIRD, K.C., THOMAS, M.K., HANLEY, T.C. & TURNER, C.B. (2011). Toward an integration of evolutionary biology and ecosystem science. *Ecology Letters* **14**, 690–701.

MCART, S.H., COOK-PATTON, S.C. & THALER, J.S. (2012). Relationships between arthropod richness, evenness, and diversity are altered by complementarity among plant genotypes. *Oecologia* **168**, 1013–1021.

MIMURA, M., YAHARA, T., FAITH, D.P., VÁZQUEZ-DOMÍNGUEZ, E., COLAUTTI, R.I., ARAKI, H., JAVADI, F., NÚÑEZ-FARFÁN, J., MORI, A.S., ZHOU, S., HOLLINGSWORTH, P.M., NEAVES, L.E., FUKANO, Y., SMITH, G.F., SATO, Y.-I., ET AL. (2016). Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evolutionary Applications* **10**, 121–139.

MORRISSEY, M.B. (2016*a*). Meta-analysis of magnitudes, differences and variation in evolutionary parameters. *Journal of Evolutionary Biology* **29**, 1882–1904.

MORRISSEY, M.B. (2016*b*). Rejoinder: Further considerations for meta-analysis of transformed quantities such as absolute values. *Journal of Evolutionary Biology* **29**, 1922–1931.

NAEEM, S., THOMPSON, LINDSEY J, LAWLER, SHARON P, LAWTON, JOHN H & WOODFIN, RICHARD M (1994). Declining biodiversity can alter the performance of ecosystems. *Nature* **368**, 734–737.

NAKAGAWA, S. & CUTHILL, I.C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* **82**, 591–605.

NAKAGAWA, S. & SANTOS, E.S.A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology* **26**, 1253–1274.

NELL, C.S., MEZA-LOPEZ, M.M., CROY, J.R., NELSON, A.S., MOREIRA, X., PRATT, J.D. & MOONEY, K.A. (2018). Relative effects of genetic variation sensu lato and sexual dimorphism on plant traits and associated arthropod communities. *Oecologia* **187**, 389–400.

NOBLE, D.W.A., LAGISZ, M., O'DEA, R.E. & NAKAGAWA, S. (2017). Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. *Molecular Ecology* **26**, 2410–2425.

ODLING-SMEE, J., LALAND, K.N. & FELDMAN, M.W. (2003). *Niche construction the neglected process in evolution.* Princeton University Press.

PAINE, R.T. (1969). A note on trophic complexity and community stability. *The American Naturalist* **103**, 91–93.

PALKOVACS, E.P., FRYXELL, D.C., TURLEY, N.E. & POST, D.M. (2015). Ecological effects of intraspecific consumer biodiversity for aquatic communities and ecosystems. In *Aquatic Functional Biodiversity* pp. 37–51. Elsevier.

PALKOVACS, E.P., MARSHALL, M.C., LAMPHERE, B.A., LYNCH, B.R., WEESE, D.J., FRASER, D.F., REZNICK, D.N., PRINGLE, C.M. & KINNISON, M.T. (2009). Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philosophical Transactions of the Royal Society B-Biological Sciences* **364**, 1617–1628.

PALKOVACS, E.P. & POST, D.M. (2009). Experimental evidence that phenotypic divergence in predators drives community divergence in prey. *Ecology* **90**, 300–305.

PINHEIRO, J., BATES, D., DEBROY, S., SARKAR, D. & R CORE TEAM (2014). nlme: linear and nonlinear mixed effects models. R package version 3.1-117.

POST, D.M., PALKOVACS, E.P., SCHIELKE, E.G. & DODSON, S.I. (2008). Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology* **89**, 2019–2032.

PRATT, J.D., DATU, A., TRAN, T., SHENG, D.C. & MOONEY, K.A. (2017). Genetically based latitudinal clines in *Artemisia californica* drive parallel clines in arthropod communities. *Ecology* **98**, 79–91.

PREGITZER, C.C., BAILEY, J.K. & SCHWEITZER, J.A. (2013). Genetic by environment interactions affect plant-soil linkages. *Ecology and Evolution* **3**, 2322–2333.

REISS, J., BRIDLE, J.R., MONTOYA, J.M. & WOODWARD, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution* **24**, 505–514.

RENNEVILLE, C., ROUZIC, A.L., BAYLAC, M., MILLOT, A., LOISEL, S. & EDELINE, E. (2016). Morphological drivers of trophic cascades. *Oikos* **125**, 1193–1202.

ROBINSON, K.M., INGVARSSON, P.K., JANSSON, S. & ALBRECTSEN, B.R. (2012). Genetic variation in functional traits influences arthropod community composition in aspen (*Populus tremula L.*). *PLoS ONE* **7**, e37679.

RODRIGUEZ-CABAL, M.A., BARRIOS-GARCIA, M.N., RUDMAN, S.M., MCKOWN, A.D., SATO, T. & CRUTSINGER, G.M. (2017). It is about time: genetic variation in the timing of leaf-litter inputs influences aquatic ecosystems. *Freshwater Biology* **62**, 356–365.

ROYAUTÉ, R. & PRUITT, J.N. (2015). Varying predator personalities generates contrasting prey communities in an agroecosystem. *Ecology* **96**, 2902–2911.

RUDGERS, J.A. & WHITNEY, K.D. (2006). Interactions between insect herbivores and a plant architectural dimorphism. *Journal of Ecology* **94**, 1249–1260.

RUDMAN, S.M., RODRIGUEZ-CABAL, M.A., STIER, A., SATO, T., HEAVYSIDE, J., EL-SABAAWI, R.W. & CRUTSINGER, G.M. (2015). Adaptive genetic variation mediates bottom-up and top-down control in an aquatic ecosystem. *Proceedings of the Royal Society B: Biological Sciences* **282**, 125–132.

RUDMAN, S.M. & SCHLUTER, D. (2016). Ecological impacts of reverse speciation in threespine stickleback. *Current Biology* **26**, 490–495.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013*a*). Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology* **94**, 1046–1056.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013*b*). Population structure determines functional differences among species and ecosystem processes. *Nature Communications* **4**.

SCHMITZ, O.J., HAWLENA, D. & TRUSSELL, G.C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13**, 1199–1209.

SCHMITZ, O.J., RAYMOND, P.A., ESTES, J.A., KURZ, W.A., HOLTGRIEVE, G.W., RITCHIE, M.E., SCHINDLER, D.E., SPIVAK, A.C., WILSON, R.W., BRADFORD, M.A., CHRISTENSEN, V., DEEGAN, L., SMETACEK, V., VANNI, M.J. & WILMERS, C.C. (2014). Animating the carbon cycle. *Ecosystems* **17**, 344–359.

SCHWEITZER, J.A., BAILEY, J.K., FISCHER, D.G., LEROY, C.J., LONSDORF, E.V., WHITHAM, T.G. & HART, S.C. (2008). Plant–soil–microorganism interactions: heritable relationship between plant genotype and associated soil microorganisms. *Ecology* **89**, 773–781.

SEMCHENKO, M., SAAR, S. & LEPIK, A. (2017). Intraspecific genetic diversity modulates plant-soil feedback and nutrient cycling. *New Phytologist* **216**, 90–98.

SENIOR, A.M., GRUEBER, C.E., KAMIYA, T., LAGISZ, M., O'DWYER, K., SANTOS, E.S.A. & NAKAGAWA, S. (2016). Heterogeneity in ecological and evolutionary meta-analyses: its magnitude and implications. *Ecology* **97**, 3293–3299.

SHIPLEY, B. (2000). *Cause and correlation in biology: a user's guide to path analysis, structural equation and causal inference.* Cambridge University Press.

SIEFERT, A., VIOLLE, C., CHALMANDRIER, L., ALBERT, C.H., TAUDIERE, A., FAJARDO, A., AARSSEN, L.W., BARALOTO, C., CARLUCCI, M.B., CIANCIARUSO, M.V., DE L. DANTAS, V., DE BELLO, F., DUARTE, L.D.S., FONSECA, C.R., FRESCHET, G.T., ET AL. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**, 1406–1419.

SILFVER, T., KONTRO, M., PAASO, U., KARVINEN, H., KESKI-SAARI, S., KEINÄNEN, M., ROUSI, M. & MIKOLA, J. (2018). Intrapopulation genotypic variation in leaf litter chemistry does not control microbial abundance and litter mass loss in silver birch, *Betula pendula*. *Plant and Soil* **426**, 253–266.

SILFVER, T., MIKOLA, J., ROUSI, M., ROININEN, H. & OKSANEN, E. (2007). Leaf litter decomposition differs among genotypes in a local *Betula pendula* population. *Oecologia* **152**, 707–714.

SILFVER, T., PAASO, U., RASEHORN, M., ROUSI, M. & MIKOLA, J. (2015). Genotype x herbivore effect on leaf litter decomposition in *Betula Pendula* saplings: ecological and evolutionary consequences and the role of secondary metabolites. *PLoS One* **10**.

SILFVER, T., ROUSI, M., OKSANEN, E. & ROININEN, H. (2014). Genetic and environmental determinants of insect herbivore community structure in a *Betula pendula* population. *F1000Research* **3**, 34–34.

SOUTHWOOD, T.R., BROWN, V.K. & READER, P.M. (1979). The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean Society* **12**, 327–348.

STHULTZ, C.M., WHITHAM, T.G., KENNEDY, K., DECKERT, R. & GEHRING, C.A. (2009). Genetically based susceptibility to herbivory influences the ectomycorrhizal fungal communities of a foundation tree species. *New Phytologist* **184**, 657–667.

TACK, A.J.M., OVASKAINEN, O., PULKKINEN, P. & ROSLIN, T. (2010). Spatial location dominates over host plant genotype in structuring an herbivore community. *Ecology* **91**, 2660–2672.

TACK, A.J.M. & ROSLIN, T. (2011). The relative importance of host-plant genetic diversity in structuring the associated herbivore community. *Ecology* **92**, 1594–1604.

TOVAR-SANCHEZ, E., VALENCIA-CUEVAS, L., CASTILLO-MENDOZA, E., MUSSALI-GALANTE, P., PEREZ-RUIZ, R.V. & MENDOZA, A. (2013). Association between individual genetic diversity of two oak host species and canopy arthropod community structure. *European Journal of Forest Research* **132**, 165–179.

TRAP, J., HÄTTENSCHWILER, S., GATTIN, I. & AUBERT, M. (2013). Forest ageing: An unexpected driver of beech leaf litter quality variability in European forests with strong consequences on soil processes. *Forest Ecology and Management* **302**, 338–345.

UTSUMI, S. (2015). Feeding evolution of a herbivore influences an arthropod community through plants: implications for plant-mediated eco-evolutionary feedback loop. *Journal of Ecology* **103**, 829–839.

VANNI, M.J. (2002). Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* **33**, 341–370.

VELLEND, M. (2005). Species diversity and genetic diversity: parallel processes and correlated patterns. *The American Naturalist* **166**, 199–215.

VELLEND, M. & GEBER, M.A. (2005). Connections between species diversity and genetic diversity. *Ecology Letters* **8**, 767–781.

VIOLLE, C., ENQUIST, B.J., MCGILL, B.J., JIANG, L., ALBERT, C.H., HULSHOF, C., JUNG, V. & MESSIER, J. (2012). The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* **27**, 244–252.

VIOLLE, C., NAVAS, M.-L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. & GARNIER, E. (2007). Let the concept of trait be functional! *Oikos* **116**, 882–892.

WAGG, C., BOLLER, B., SCHNEIDER, S., WIDMER, F. & VAN DER HEIJDEN, M.G.A. (2015). Intraspecific and intergenerational differences in plant-soil feedbacks. *Oikos* **124**, 994–1004.

WALSH, M.R., DELONG, J.P., HANLEY, T.C. & POST, D.M. (2012). A cascade of evolutionary change alters consumer-resource dynamics and ecosystem function. *Proceedings of the Royal Society B-Biological Sciences* **279**, 3184–3192.

WANG, X.-Y., MIAO, Y., YU, S., CHEN, X.-Y. & SCHMID, B. (2014). Genotypic diversity of an invasive plant species promotes litter decomposition and associated processes. *Oecologia* **174**, 993–1005.

WEIS, J.J. & POST, D.M. (2013). Intraspecific variation in a predator drives cascading variation in primary producer community composition. *Oikos* **122**, 1343–1349.

WERNER, E.E. & PEACOR, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**, 1083–1100.

WHITHAM, T.G., BAILEY, J.K., SCHWEITZER, J.A., SHUSTER, S.M., BANGERT, R.K., LEROY, C.J., LONSDORF, E.V., ALLAN, G.J., DIFAZIO, S.P., POTTS, B.M., FISCHER, D.G., GEHRING, C.A., LINDROTH, R.L., MARKS, J.C., HART, S.C., ET AL. (2006). A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* **7**, 510–523.

WHITHAM, T.G., YOUNG, W.P., MARTINSEN, G.D., GEHRING, C.A., SCHWEITZER, J.A., SHUSTER, S.M., WIMP, G.M., FISCHER, D.G., BAILEY, J.K., LINDROTH, R.L., WOOLBRIGHT, S. & KUSKE, C.R. (2003). Community and ecosystem genetics: A consequence of the extended phenotype. *Ecology* **84**, 559–573.

WILKINSON, A., ALEXANDER, I. & JOHNSON, D. (2012). Genotype identity determines productivity and CO2 efflux across a genotype-species gradient of ectomycorrhizal fungi. *Fungal Ecology* **5**, 571–580.

WILKINSON, A., SOLAN, M., TAYLOR, A.F.S., ALEXANDER, I.J. & JOHNSON, D. (2010). Intraspecific diversity regulates fungal productivity and respiration. *Plos One* **5**, e12604.

ZYTYNSKA, S.E., FAY, M.F., PENNEY, D. & PREZIOSI, R.F. (2011). Genetic variation in a tropical tree species influences the associated epiphytic plant and invertebrate communities in a complex forest ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 1329–1336.

ZYTYNSKA, S.E., KHUDR, M.S., HARRIS, E. & PREZIOSI, R.F. (2012). Genetic effects of tank-forming bromeliads on the associated invertebrate community in a tropical forest ecosystem. *Oecologia* **170**, 467–475.

Supplementary information for Chapter III.

Appendix III.S1. List of references used in the meta-analysis. Full references are included in the main text reference list.

List of references for the analyses of intraspecific variation

Barbour et al., 2009*b*, 2009*a*, 2016
Barbour, Storer & Potts, 2009*c*
Barrios-Garcia et al., 2016
Bassar et al., 2010
Burkle et al., 2013
Bustos-Segura et al., 2017
Chislock et al., 2013
Cornelissen et al., 2000
Classen et al., 2007
Crutsinger et al., 2006, 2008*b*
Crutsinger et al., 2009*a*
Crutsinger et al., 2014*a*, 2014*b*
Crutsinger, Carter & Rudgers, 2013
Crutsinger, Sanders & Classen, 2009*b*
de Graaff et al., 2013
Des Roches et al., 2013
El-Sabaawi et al., 2015
Farkas et al., 2013
Fryxell et al., 2015
Goitom et al., 2018
Harmon et al., 2009
Harrison et al., 2018
Hines et al., 2014
Huang et al., 2015
Ingram et al., 2012
Ito & Ozaki, 2005
Jackrel & Wootton, 2014
Johnson & Agrawal, 2005
Johnson et al., 2006
Johnson, Vellend & Stinchcombe, 2009
Kagiya et al., 2018
Katano, 2011
Lagerstrom, Nilsson & Wardle, 2013
Lecerf & Chauvet, 2008
LeRoy et al., 2007
Madritch & Hunter, 2005
Madritch & Lindroth, 2011
Madritch et al., 2009
Madritch, Donaldson & Lindroth, 2006
Matthews et al., 2016

Nell et al., 2018
Palkovacs & Post, 2009
Palkovacs et al., 2009
Post et al., 2008
Pratt et al., 2017
Pregitzer, Bailey & Schweitzer, 2013
Renneville et al., 2016
Robinson et al., 2012
Rodriguez-Cabal et al., 2017
Royauté & Pruitt, 2015
Rudgers & Whitney, 2006
Rudman & Schluter, 2016
Rudman et al., 2015
Rudolf & Rasmussen, 2013*a*, 2013*b*
Schweitzer et al., 2008
Silfver et al., 2007, 2014, 2015, 2018
Sthultz et al., 2009
Tack et al., 2010
Tovar-Sanchez et al., 2013
Trap et al., 2013
Utsumi, 2015
Wagg et al., 2015
Walsh et al., 2012
Weis & Post, 2013
Zytynska et al., 2011, 2012

List of references for the analyses of intraspecific richness

Abbott et al., 2017
Burkle et al., 2013
Campos-Navarrete et al., 2015
Cook-Patton et al., 2011
Crawford & Rudgers, 2013
Crutsinger et al., 2006, 2008*a*, 2008*b*, 2009*b*
Genung et al., 2010
Hughes, 2014
Johnson et al., 2006
Kanaga et al., 2009
Kotowska, Cahill Jr & Keddie, 2010
Madritch & Hunter, 2003, 2004
Madritch et al., 2006
McArt, Cook-Patton & Thaler, 2012
Semchenko, Saar & Lepik, 2017
Tack & Roslin, 2011

Wang et al., 2014
Wilkinson et al., 2010
Wilkinson, Alexander & Johnson, 2012

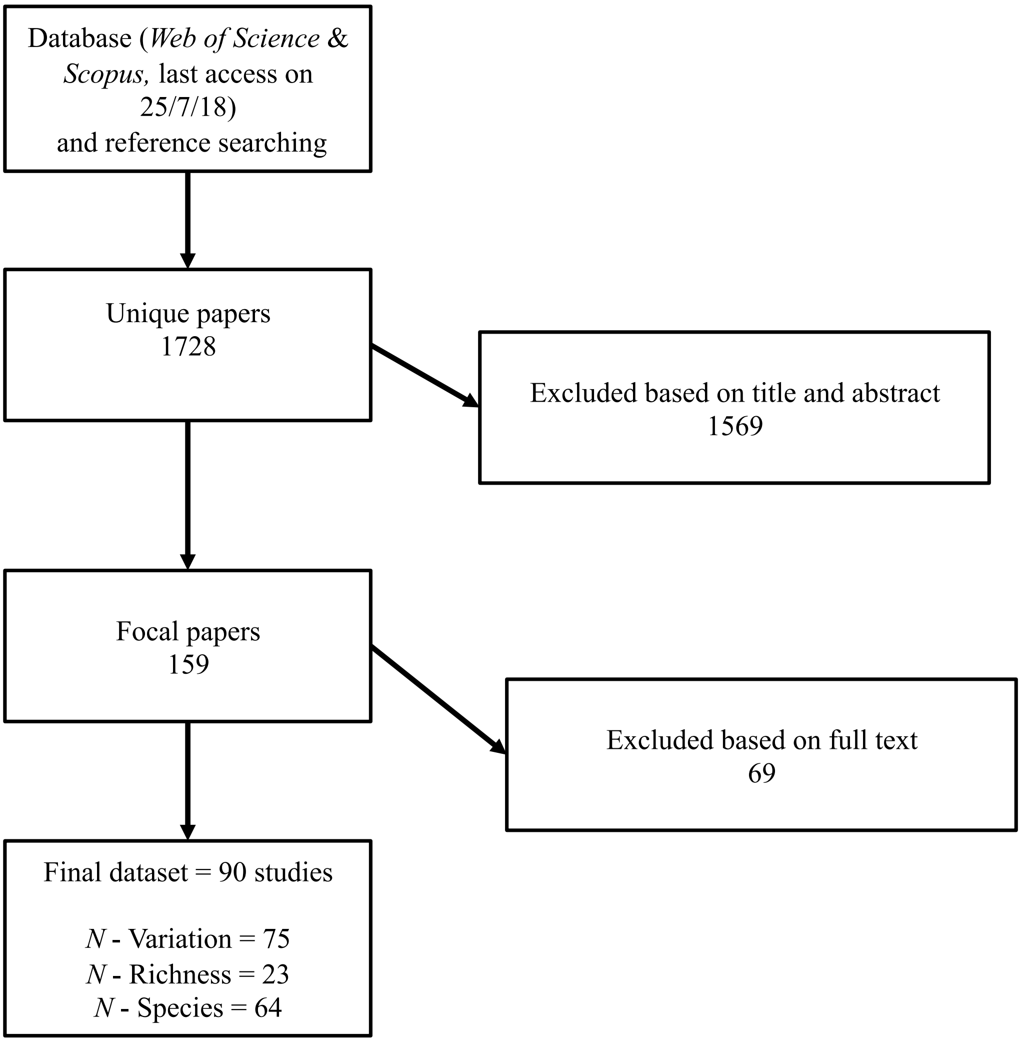


Figure III.S1. Flow diagram of manuscript screening and eligibility for this meta-analysis.

Table III.S1. Formulae used to convert different statistical values into an *r* correlation coefficient (Koricheva *et al*., 2013; Nakagawa & Cuthill, 2007).

Statistic	Formula used to convert or approximate *r*
t	$\sqrt{\frac{t^2}{t^2+df}}$
F	$\sqrt{\frac{df_nF}{df_nF+df_d}}$
X2	$\sqrt{\frac{X^2}{N}}$
Hedges' g	$\sqrt{\frac{g^2n_1n_2}{g^2n_1n_2+(n_1n_2)df}}$
R2	$\sqrt{\frac{1-((n-1)*(1-R2))}{n-k-1}}$

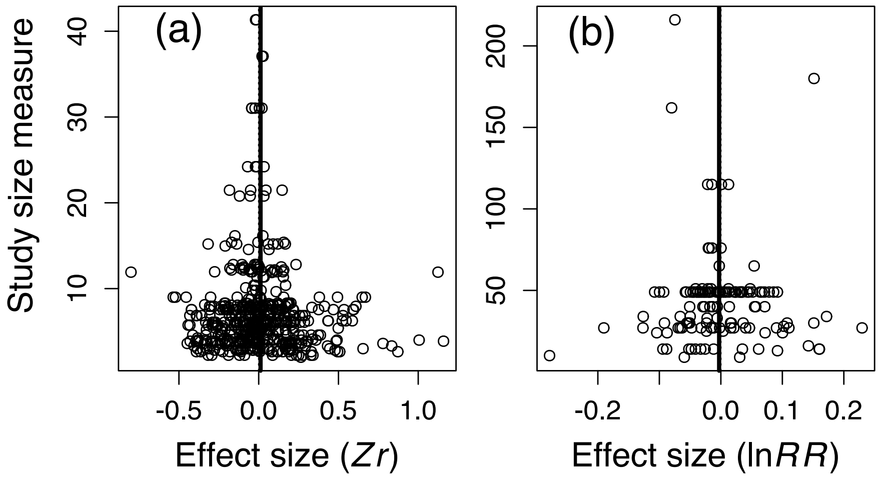


Figure III.S2. Funnel plots describing the residuals effect size (see main text for details) distribution against an estimation of the study size (the inverse of se_{Zr} and the sample size, respectively) for **(a)** intraspecific *variation* and **(b)** intraspecific *richness*.

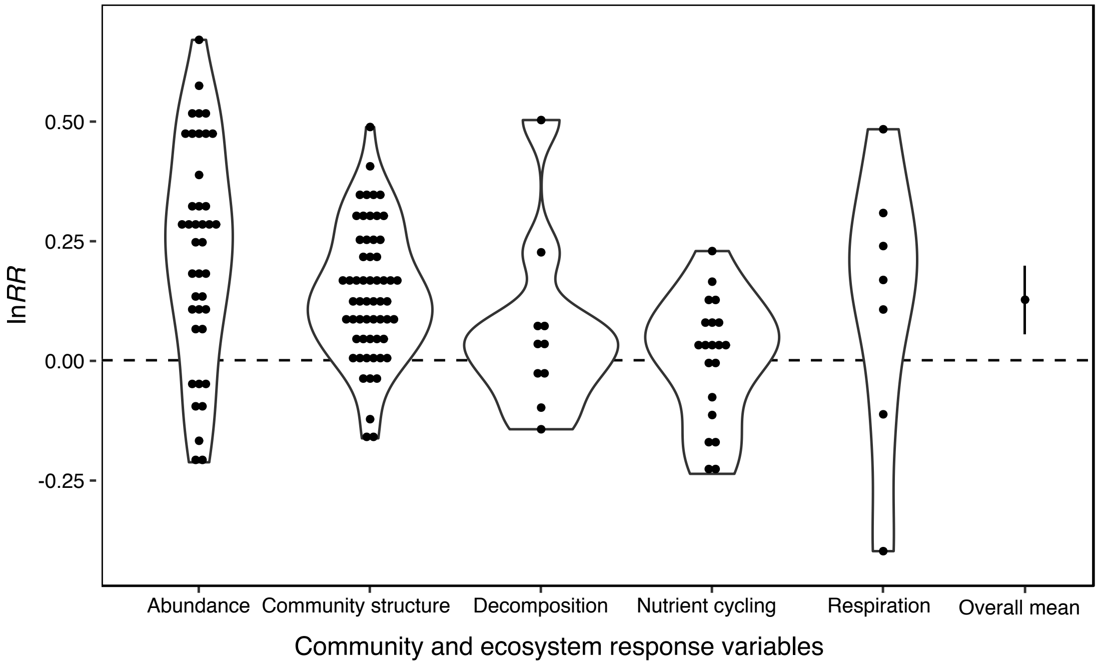


Figure III.S3. Distribution of the effect sizes (ln*RR*) across ecological metrics. The overall mean and 95% confidence interval (represented by the error bar) was calculated using a linear mixed-effect model with article ID and monoculture ID as random factors, and the reverse of sample size as weighting parameter.

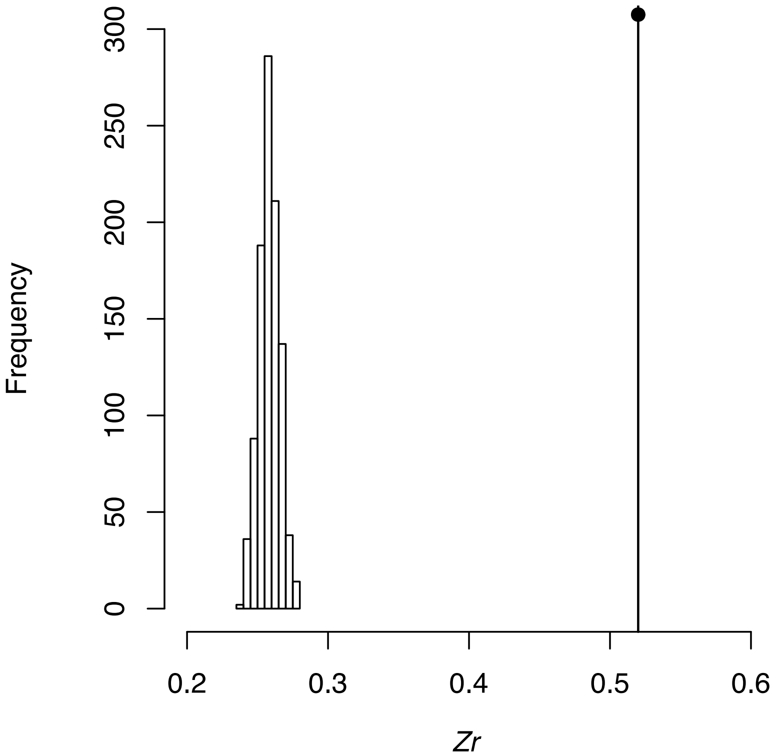


Figure III.S4. Distribution of resampled mean effect size (MES) expected under the null hypothesis, i.e. the effect of intraspecific variation in all studies is zero. The vertical straight line represents the observed MES.

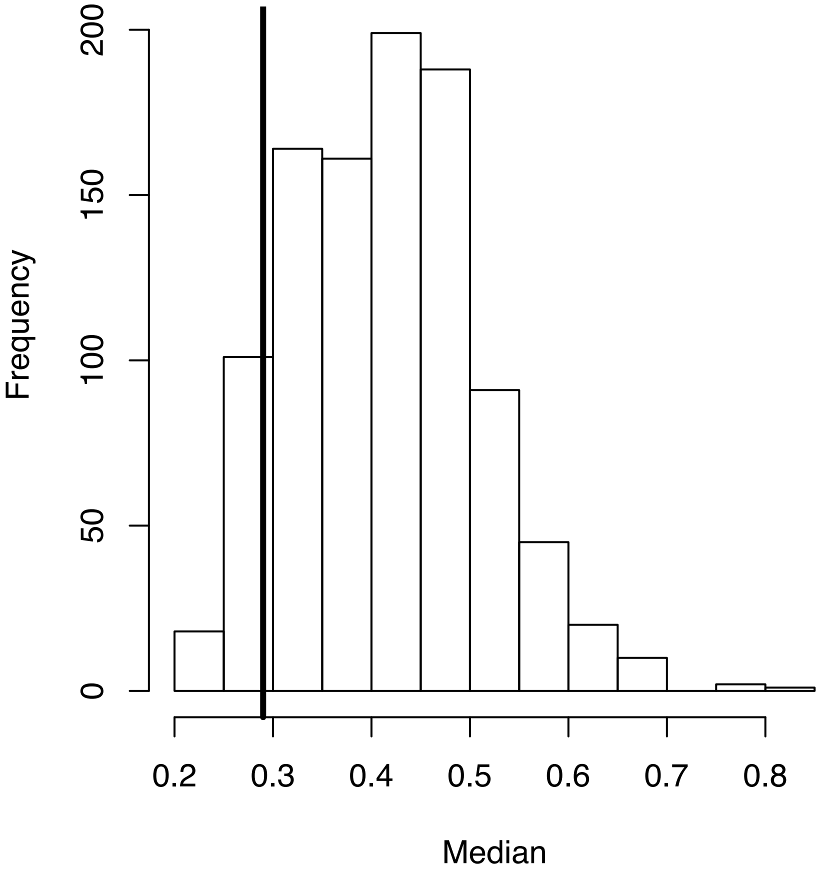


Figure III.S5. Distribution of median effect sizes calculated for each of the 1000 sets of 15 studies randomly selected within our extended data set of 75 studies. The vertical straight line represents the median effect size for the 15 studies in common between our extended data set and that used by Des Roches *et al.* (2018).

Chapitre IV.

Functional traits variability and their covariations

Chapter adapted from an article published in **Proceedings of the Royal Society B**, and from an article submitted for publication in **Ecology and Evolution**.

Résumé

La variabilité phénotypique est de plus en plus étudiée au travers des traits fonctionnels réponses et d'effets. Ceux-ci procurent un cadre mécaniste pour étudier la réponse des organismes faces aux contraintes environnementales et les effets de ces réponses sur le fonctionnement des écosystèmes. Les covariations entre traits réponses et traits effets ont été peu étudiées au niveau intraspécifique, alors que cela pourrait expliquer la façon dont les variations phénotypiques affectent les écosystèmes. Dans une première partie nous avons défini un syndrome fonctionnel liant les traits réponses et effets. Ce syndrome pourrait permettre de mieux comprendre les effets écologiques de la variabilité phénotypique sur les niveaux d'organisations biologiques plus élevés, et de faire un lien entre l'écologie évolutive et l'écologie des écosystèmes. Dans une deuxième partie nous avons quantifié la variabilité de quatre traits fonctionnels (masse corporelle, taux d'excrétion et métabolique, et comportement), leurs covariations, et les syndromes émergeant entre treize populations de vairons (*Phoxinus phoxinus*). Ensuite, nous avons testé si les traits et leurs covariations – formant des syndromes - étaient dépendants des relations phylogénétiques entre populations ou de l'environnement local (température, prédation) ; et si des processus adaptatifs (plasticité ou sélection) ou non-adaptatifs (dérive génétique) étaient impliqués. Les résultats ont montré que les traits, leurs covariations et les syndromes émergeant étaient variables entre les populations. De plus, la température et la prédation étaient impliquées dans la variabilité de la covariation entre la masse corporelle et le métabolisme au travers de processus adaptatifs (plasticité ou sélection). La variabilité des autres covariations était probablement due à la dérive génétique. Nous avons conclu que les syndromes entre traits fonctionnels étaient spécifiques aux populations, et qu'à la fois des processus adaptatifs et non-adaptatifs modulaient les traits fonctionnels. Etant donné le rôle central des traits fonctionnels, les différences de syndromes fonctionnels au sein d'une espèce apportent des perspectives intéressantes concernant le rôle écologique de la diversité intraspécifique.

Abstract

Phenotypic variability is increasingly assessed through functional response and effect traits, which provide a mechanistic framework for investigating how an organism responds to varying ecological factors and how these responses affect ecosystem functioning. Covariation between response and effect traits has been poorly examined at the intraspecific level, thus hampering progress in understanding how phenotypic variability alters the role of organisms in ecosystems. In a first part we defined a functional syndrome linking response and effect traits. This syndrome might improve our understanding of the ecological impacts of phenotypic variation among individuals in wild populations across levels of biological organisation, and the linkage between ecosystem and evolutionary ecology. In a second part, we quantified and compared the variability in four functional traits (body mass, metabolic rate, excretion rate and boldness), their covariations and the subsequent syndromes among thirteen populations of a common freshwater fish (the European minnows, *Phoxinus phoxinus*). We then tested whether functional traits and their covariations - forming syndromes - were undermined by the phylogenetic relatedness among populations (historical effects) or the local environment (i.e., temperature and predation pressure), and whether adaptive (selection or plasticity) or non-adaptive (genetic drift) processes sustained variations among populations. We found substantial among-populations variability in functional traits, trait covariations and in the emerging syndromes. We further found that adaptive mechanisms (plasticity and/or selection) related to water temperature and predation pressure modulated the covariation between body mass and metabolic rate. Other trait covariations were more likely driven by genetic drift, suggesting that non-adaptive processes can also lead to substantial differences in trait covariations among populations. Overall, we concluded that syndromes among functional traits are population-specific, and that both adaptive and non-adaptive processes are shaping functional traits within structured riverscapes. Given the pivotal role of functional traits, differences in functional syndromes within species provide interesting perspectives regarding the role of intraspecific diversity for ecosystem functioning.

Part I.
The functional syndrome: linking individual trait variability to ecosystem functioning.

Allan Raffard[1,2,3], Lecerf Antoine[2], Cote Julien[3], Buoro Mathieu[4], Lassus Remy[3], & Cucherousset Julien[3].

[1] CNRS, Université Toulouse III Paul Sabatier, Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UMR-5321, F-09200 Moulis, France.

[2] EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France.

[3] Laboratoire Évolution et Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, IRD, UPS, 118 route de Narbonne, Toulouse 31062, France.

[4] ECOBIOP, INRA, Univ.Pau and Pays Adour, 64310 St Pée-sur-Nivelle, France

Adapted from an article published in **Proceedings of the Royal Society B**.

While trait variability among individuals has been historically accounted for in evolutionary sciences, it has merely been seen as noise around the average phenotype of a species by community and ecosystem ecologists (Bolnick *et al.*, 2003, 2011; Violle *et al.*, 2012). Recent advances have, however, suggested that not only organism phenotypes are affected by their environment, but that they can reciprocally act on it (Odling-Smee, Laland, & Feldman, 2003; Bolnick *et al.*, 2011), coupling ecological and evolutionary processes in a dynamic relationship (Pelletier, Garant, & Hendry, 2009; Matthews *et al.*, 2014; Hendry, 2016). In this context, the ecological consequences of intraspecific phenotypic variability are increasingly recognised, and recent studies have demonstrated broad consequences of phenotypic variability on key ecosystem processes such as primary production and leaf litter decomposition (Bassar *et al.*, 2010; Rudolf & Rasmussen, 2013a, 2013b; El-Sabaawi *et al.*, 2015a). To date, however, most studies have focused on the ecosystem effects of a single phenotypic trait (e.g. morphology, body mass) despite the fact that individuals can simultaneously vary in multiple phenotypic traits (Sih, Bell, & Johnson, 2004) (but see for instance Bassar *et al.*, 2010). Therefore, a multi-trait approach is needed to provide an integrative understanding of the effects of individuals on ecosystems.

From a functional perspective, phenotypic traits have been classified as functional effect traits or functional response traits (Violle *et al.*, 2007; Díaz *et al.*, 2013). On one hand, functional effect traits determine how and to what extent an organism influences energy flow and matter transformation in an ecosystem (Díaz *et al.*, 2013). For instance, nitrogen excretion rate is considered as an effect trait because it induces changes in nutrient availability resulting in altered algal growth, thus modifying primary productivity (El-Sabaawi *et al.*, 2015b). On the other hand, functional response traits determine how an organism responds to environmental conditions (Violle *et al.*, 2007; Díaz *et al.*, 2013). For instance, presence of predators may reduce individual activity (Wooster & Sih, 1995), therefore activity level is considered as a response trait. Studies linking intraspecific trait variability to ecosystem functioning have mostly focused on response trait variations (e.g. sex ratio Fryxell *et al.*, 2015, morphology Harmon *et al.*, 2009, or behaviour Royauté & Pruitt, 2015). However, response traits and ecosystem processes are not proximately related and, therefore, such relationships are conditional on covariations between response and effect traits. For instance, phenotypic variations in guppies (*Poecilia reticuata*) has been demonstrated to impact primary productivity through a correlation between individual life history and nitrogen excretion rate (Bassar *et al.*, 2010).

Evolutionary biologists have shed light on various patterns of covariations in life history and behavioural traits. These correlations among phenotypic traits are termed *syndrome*, including the life history and behavioural syndromes (Roff, 1992; Sih *et al.*, 2004). The 'Pace Of Life Syndrome' hypothesis further states that trait covariation extends over several phenotypic aspects including the life history, behaviour and physiology of organisms (Reale *et al.*, 2010). These syndromes are best understood as having emerged from evolutionary processes and, therefore, lack relevance to infer the relationship between response and effect traits which are underlined in eco-evolutionary dynamics (Pelletier *et al.*, 2009; Hendry, 2016). This leads us to introduce the concept of 'functional syndrome', which we define as the association between correlated suites of response and effect traits (i.e. between a 'response syndrome' and an 'effect syndrome', Figure IV.1). The dependence of effect traits upon response traits may arise from metabolic and stoichiometric constraints (metabolic theory of ecology Brown *et al.*, 2004, and ecological stoichiometry Leal, Seehausen, & Matthews, 2016). For instance, fast-paced individuals with high metabolic and nutrient requirements are expected to exert stronger top-down control on their resources than slow-growing individuals. Nutrient immobilization - contributing to growth rate - may result in a slower rate of nutrient excretion of fast-paced individuals than slow-paced individuals (Leal, *et al.*, 2016).

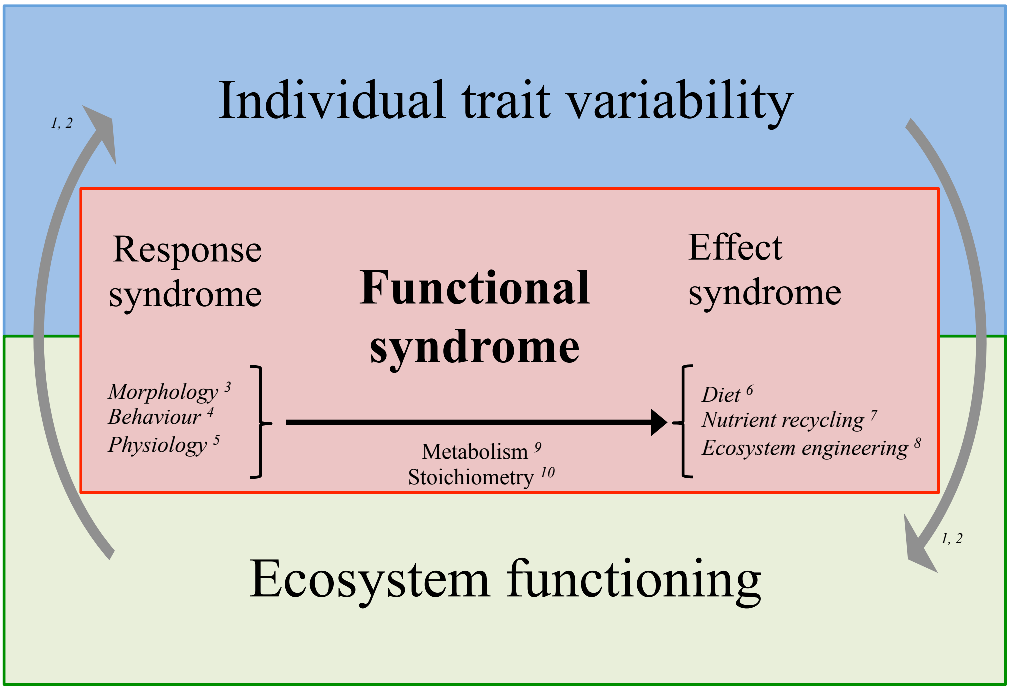


Figure IV.1. Conceptual representation of the functional syndrome. Association between response and effect traits (represented by the central arrow) is at the core of the interactions between individual trait variability and ecosystem functioning that are linked through eco-evolutionary dynamics (represented by the grey arrows). Examples of categories of response traits (through which individuals adapt to their environment) and of effect traits (by which individuals act on their ecosystem) are provided under their respective syndrome. The superscripts refer to cited references. Superscripts indicate references: 1. Pelletier *et al.*, 2009; 2. Hendry, 2016; 3. Harmon *et al.*, 2009; 4. Biro, Adriaenssens, & Sampson, 2014; 5. Ketterson, Atwell, & McGlothlin, 2009; 6. Bolnick *et al.*, 2003; 7. Vanni, 2002; 8. Matthews *et al.*, 2014; 9. Brown *et al.*, 2004; 10. Leal, *et al.*, 2016.

This functional syndrome may represent an underappreciated link between genetic and environmental factors acting on individuals (Torres-Dowdall *et al.*, 2012) and the consequences of individuals on their environment (Violle *et al.*, 2007). This confirms the essential role of functional traits in eco-evolutionary dynamics (Leal, *et al.*, 2016), where variations in response traits are the basis for organisms to evolve when facing environmental variability and where the subsequent covariation with effect traits can influence environmental conditions (Figure IV.1). Consequently, the functional syndrome should provide novel insights into eco-evolutionary studies and could therefore represent a new linkage between ecosystem and evolutionary ecology (Matthews *et al.*, 2014). To test for the existence of a functional syndrome and fully embrace the importance of phenotypic variability for ecosystems, we suggest using a multi-trait and multi-step approach. First, we recommend measuring several phenotypic traits on each individual and explicitly discriminating response and effect trait when designing individual phenotypic studies. Second, associations among response traits (response syndrome) and effects traits (effect syndrome) should be tested independently. Third, linkage between the two aforementioned syndromes should be tested. While the repeatability of traits involved can inform on the stability of impacts of intraspecific trait variability on ecosystem functioning, we suggest that functional syndromes may result from correlations among traits arising from both intra-individual and inter-individual covariations of traits (Brommer, 2013; Brommer & Class, 2017) and might therefore not require the repeatability of all traits involved in the syndrome. The functional syndrome may further vary with the environmental contexts, due to selective pressures and plastic changes, even if its structure in a given context is still crucial for ecosystem functioning. Quantifying the temporal consistency and environmental dependency of the functional syndrome should provide an integrative understanding of the ecosystemic importance of phenotypic variability.

Part II.
Variability of functional traits and their syndromes in a freshwater fish species (*Phoxinus phoxinus*): the role of adaptive and non-adaptive processes.

Allan Raffard[1,2], Julien Cucherousset[3], Jérôme G. Prunier[1], Géraldine Loot[3], Frédéric Santoul[2], & Simon Blanchet[1].

[1] *CNRS, Université Toulouse III Paul Sabatier, Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UMR-5321, F-09200 Moulis, France.*

[2] *EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France.*

[3] *Laboratoire Évolution et Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, IRD, UPS, 118 route de Narbonne, Toulouse 31062, France.*

Article accepted with minor revisions in **Ecology and Evolution**.

Introduction

Phenotypic variability measured within species has historically been the core of evolutionary studies, as it constitutes the visible outcome of evolutionary processes (Darwin, 1859; Roff, 1992; Stearns, 1992). It is now increasingly acknowledged that intraspecific phenotypic variability can have important ecological consequences notably for community structure and ecosystem functioning (Chapter III; Des Roches *et al.*, 2018). Indeed, *functional traits* are extremely important for organism adaptation and for predicting how organisms affect their own biotic and abiotic environment (Violle *et al.*, 2007; Díaz *et al.*, 2013). Functional traits display variability both within and among populations (Villéger *et al.*, 2017; Helsen *et al.*, 2017). For instance, the nutrient excretion rate (a trait potentially affecting nutrient availability in ecosystems, Vanni 2002) can vary substantially among and within populations (Villéger *et al.*, 2012; Evangelista *et al.*, 2017). Since functional traits determine the way organisms interact with -and modulate- the environment, it is important to investigate the spatial distribution of functional traits (Funk *et al.*, 2016; Villéger *et al.*, 2017).

Average functional trait values can vary across landscapes. For instance the metabolic rate of ectotherms is, on average, higher in warm than in cold environments (Brown *et al.*, 2004; Hildrew, Raffaelli, & Edmonds-Browns, 2007). Nonetheless, variability in traits can also be quantified through the covariations existing among traits (Reale *et al.*, 2010), and patterns of covariations are referred to as *syndromes* (i.e. which corresponds to a set of trait covariations, Dingemanse et al. 2007). Syndromes have primarily been investigated for traits (mainly behavioural traits) related to the fitness of individuals (Reale et al. 2010), although it has recently been demonstrated that covariations also occur in functional traits, hence forming functional syndromes (ANNEXE 1). Functional syndromes have been shown to exist in several species (e.g. ANNEXE 1; Defossez *et al.* 2018), but the variability of these syndromes across populations and environmental conditions remains unexplored.

Functional syndromes are nonetheless expected to vary among populations within a single species (Peiman & Robinson, 2017). Indeed, recent works have experimentally demonstrated that environmental conditions can induce biological constrains that can modulate trait covariations and associated syndromes (Finstad *et al.*, 2007; Killen *et al.*, 2013). For instance, food availability in the environment has been demonstrated to affect covariation between metabolic rate and risk taking behaviour in the European sea bass (*Dicentrarchus labrax*) (Killen, Marras, & McKenzie, 2011). Variation in syndromes among populations have also been reported in the wild (Dingemanse *et al.*, 2007; Pruitt *et al.*, 2010; Peiman & Robinson, 2012; Zavorka *et al.*, 2017). Beyond the proximate influence of environmental characteristics (e.g. temperature, predation…) on syndromes, the evolutionary history of populations -such as the past demographic and colonization history- may also play a underestimated role in shaping syndromes (Armbruster & Schwaegerle, 1996; Peiman & Robinson, 2017). For instance, populations can harbour different syndromes because they may have been colonized by two independent lineages having evolved divergent syndromes in their past respective refuge ("the ghost of colonization past"). This past evolutionary legacy is likely to be identified at the level of the genetic lineages; two genetically-related populations being more likely to display similar syndromes than two genetically-unrelated populations. This possible evolutionary legacy of syndromes has –up to our knowledge- rarely been considered.

In this study, we investigated the variability of functional traits and the syndromes they form in wild populations inhabiting heterogeneous environments. Using a common freshwater fish species (the European minnow, *Phoxinus phoxinus*) as a model species, we aimed at testing (i) whether functional traits and their covariations vary between populations, and (ii) whether this variability is explained by environmental factors and/or the evolutionary history of populations. Focusing on four functional traits (i.e. excretion rate, metabolism, body mass and boldness), we first expected that both mean values and covariations of traits differ between populations because of contrasting environments and evolutionary histories of the selected populations. Second, we focused on two environmental characteristics (temperature and predation intensity) that affect functional traits (e.g. metabolism, Gillooly 2001), and that are hence likely to also modulate their covariations. We concomitantly tested whether the past evolutionary history of populations may contribute to explain variation in covariations among functional traits using phylogenetic models. Specifically, we assessed the relationships between genetic similarity (inferred from microsatellite markers) and syndromes similarity among populations. An influence of the environment on traits would suggest potential adaptation (or plasticity of these syndromes), and we hence finally used a quantitative genetic approach (*Pst*/*Fst*, Leinonen *et al.* 2013) to infer the evolutionary processes (genetic drift *vs*. selection/plasticity) underlying differences in trait variation and covariation among populations.

Materials and methods

Model species

The European minnow (*P. phoxinus*) is an abundant species in Western Europe in cold lakes (e.g. mountains lakes) and rivers (e.g. from small rivers at intermediate altitude to mountain streams) with summer water temperature generally lower than 22-24°C (Keith *et al.*, 2011). It is a small-bodied fish species (<12 cm long, 5-8 cm long as an adult in general) with a generalist diet composed of small invertebrates, algae or zooplankton (Frost, 1943; Collin & Fumagalli, 2011). European minnows is considered as a genotypically and phenotypically variable species (Collin & Fumagalli, 2011, 2015; Fourtune *et al.*, 2018).

Sampling sites and animal rearing

We focused on riverine European minnow populations from the Dordogne-Garonne river basin in southwestern France (Figure IV.2). We selected thirteen sites (coded from A to M) in different rivers to reflect their potential colonization history (Fourtune *et al.*, 2016; Paz-Vinas *et al.*, 2018). Sampled rivers were selected based on previous knowledge in this area in term of environmental and geographic characteristics (Fourtune *et al.* 2016, 2018).

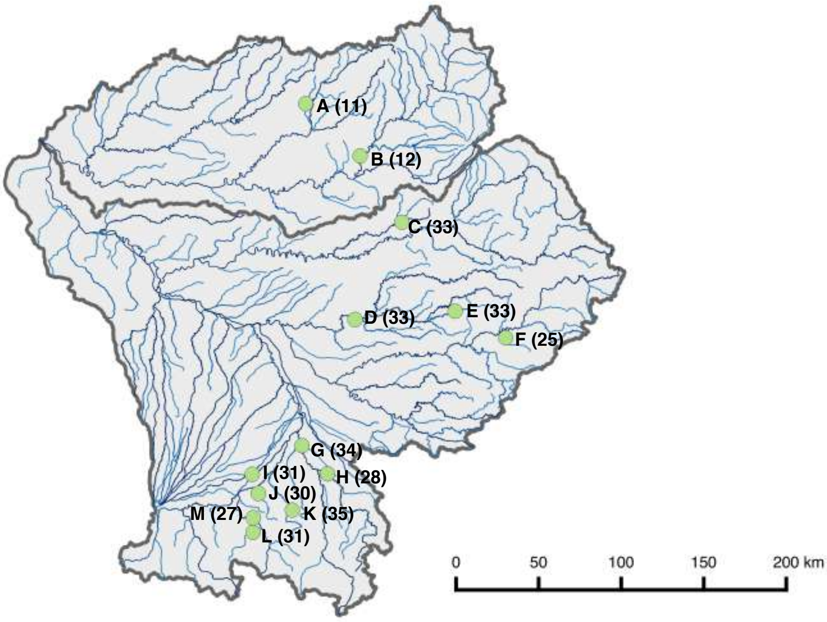


Figure IV.2. Distribution of the thirteen studied populations of European minnows (*Phoxinus phoxinus*). Names of populations were coded from A to M, the number of individuals for each population is given as indication.

For each site, we focused and measured two environmental variables that have been shown to modulate functional traits in ectotherms (Gillooly, 2001; Biro, Beckmann, & Stamps, 2010; Bestion *et al.*, 2014), and hence potentially their covariations. We first recorded water temperature, which is a key abiotic factor affecting the rate of physiological processes, especially in ectotherm organisms (Brown *et al.*, 2004). Indeed, organisms adapt phenotypically to temperature by adjusting their metabolic rate and behaviour (Gillooly, 2001; Biro *et al.*, 2010). Water temperature was measured as the mean temperature recorded from July to September 2017 using automatic sensors (HOBO®, one measure every hours). Mean summer water temperature varied from 15.5°C (site E) to 21.5°C (site D) (Figure IV.2). In addition, we measured the local predation pressure, a key biotic factor that can affect organism's phenotype (Langerhans, 2007). Specifically, predation risk can affect the physiology and behaviour of individuals by inducing strong stresses (Bell and Sih 2007, Hawlena and Schmitz 2010). Predation pressure was calculated on each site as the density of piscivorous fishes (namely northern pike, *Esox lucius*; brown trout, *Salmo trutta*; rainbow trout, *Oncorhynchus mykiss*; European perch, *Perca fluviatilis;* pikeperch*, Sander lucioperca*; and European eel, *Anguilla anguilla*). This metric was similar to that described in Edeline *et* *al.* (2013). It was calculated by dividing the number of sampled individuals predator per the surface covered during sampling to obtain an index of predation; these data -for each site- were sourced from Fourtune *et al.* (2016) and from the French Agency for Biodiversity (Poulet, Beaulaton, & Dembski, 2011).

In summer 2016, we collected adult fish on these thirteen sites using electrofishing (Figure IV.2). On each river we collected approximately a hundred of adult individuals along a ~200m long river stretch to ensure representativeness of the fish habitat. Then, we randomly sampled thirty individuals within the size range of the population (visually assessed) to have a representative sample of each population. Electrofishing and lab rearing of fish were performed under authorizations of local authorities. Fish were brought to the lab and maintained in a thermoregulated room for two to four weeks before experiments. Fish from the different populations were held in independent 150L tanks in which water temperature was set at 17°C and photoperiod at a light:dark cycle of 12:12 (Golovanov, 2013). They were fed with frozen bloodworms three times a week. Prior to experiments, fish were anesthetized (benzocaine, 25mg.L^{-1}), weighed (to the nearest 0.01g) and tagged with a Passive Integrated Transponder (PIT) tags (8 × 1.4 mm, FDX-B 'skinny' PIT tag, Oregon RFID, USA) inserted in the general cavity using a sterile scalpel. Fish recovered and acclimatized to the rearing room for 10 days before the quantification of three functional traits in addition of body mass (boldness, excretion rate and metabolic rate). Before quantification of functional traits, individuals were starved for two days to ensure the same starvation level among individuals.

Boldness

Boldness was assessed for each individual independently in circular containers (30 cm in diameter) filled with 5L of dechlorinated tap water at 17°C and 500 mL of water from tank with conspecifics. The containers were surrounded by curtains to homogenise light conditions and to hide the experimenter. A shelter (pipe, 7 cm length x 3 cm diameter) was added in each container to allow the fish to hide. After having introduced each individual into the shelter and after 10 min of acclimatization to reduce stress level induced by handling, the shelter was opened and each individual was filmed for fifteen minutes. Video footages were subsequently analysed with the software "BORIS" (Friard & Gamba, 2016). Boldness was quantified as the time spent outside of the shelter. The order and the containers in which individuals were assayed were randomly attributed. All behavioural assays were performed in the afternoon (from 12:00 p.m. to 16:00 p.m.) to minimize the potential effects of circadian rhythms.

Excretion rate

Excretion rate was quantified using nitrogen excreted by organisms as the dissolved form of ammonium NH_4^+. Changes in NH_4^+ concentration in water can affect ecosystem functioning through an increase in nutrient availability (Capps & Flecker, 2013) and primary production (Schmitz *et al.* 2010, Bassar *et al.* 2016). Following Villéger *et al.* (2012), individuals were placed in plastic bags containing 500 ml of spring bottled water for 1h at 17°C. Individuals were then removed and 100 ml of water was filtered through a glass microfiber filter (Whatman, GF/C, diameter = 25 mm), and samples were frozen at -20°C. Excretion rate (NH_4^{+-} in $\mu g.l^{-1}.h^{-1}$) was determined with a high-performance ionic chromatograph (Dionex DX-120).

Metabolic rate

We measured the oxygen consumption rate as a proxy of the metabolic rate of individuals. Fish were individually placed in a custom made metabolic chamber filled with 500 mL of dechlorinated tap water and hermetically sealed. Chambers were set in a thermoregulated room at 17°C in the dark to lower the stress level. We measured the metabolic rate just after handling so that the same stress was imposed to all individuals. Measurements of oxygen concentration were taken after 10 min, allowing individuals to acclimate, and continuously every five seconds for 50 min using oxygen probes (OXROB10, Pyroscience). The metabolic rate was calculated as the absolute slope between the oxygen quantity in the chamber and the time, reflecting the consumption of oxygen ($mg.h^{-1}$).

Genetic analyses

Thirty additional adults from each of the thirteen sites were sampled for genetic material. For each individual, we collected and preserved in 70% ethanol a small piece of pelvic fin and individuals were then released in their respective sampling site. Genomic DNA was extracted using a salt-extraction protocol (Aljanabi, 1997). Eighteen autosomal microsatellite markers were considered in this study: polymerase chain reactions (PCR) and genotyping were performed as detailed in Appendix IV.S1, resulting in a final dataset of 357 genotypes. We checked for multi-locus deviation from the Hardy-Weinberg Equilibrium (HWE) and for gametic disequilibrium using GENEPOP 4.2.1 (Rousset, 2008) after sequential Bonferroni correction to account for multiple related tests (Rice, 1989). The presence of null alleles was then assessed at each locus by analysing homozygote excess in five populations that did not follow the HWE, using MICROCHECKER 2.2.3 (Van Oosterhout *et al.*, 2004). We discarded from further analyses any locus showing significant gametic disequilibrium and/or evidence of null alleles, resulting in the withdrawal of one locus (CtoG-075), for a total number of seventeen loci.

We computed the Nei's standard genetic distance (Nei, 1973) between each pair of populations using the *diveRsity* R-package (function *diffCalc*; Keenan et al. 2013). A hierarchical cluster analysis was then performed to uncover genetic relatedness among the thirteen populations using the functions *hclust* (R-package *stats*) and *as.phylo* (R-package *ape*; Paradis *et al.* 2004) to convert the genetic dissimilarity matrix into an unrooted phylogenetic tree based on complete linkage method.

Finally, we estimated the overall level of genetic differentiation *Fst* among the thirteen populations using the R-package *hierfstat* (Goudet, 2005). The resulting global *Fst* corresponds to the inter-population variance component in allelic frequencies (Yang, 1998), and to the level of differentiation among populations due to genetic drift only (Leinonen *et al.*, 2013). This value is directly comparable to the inter-population variance component in quantitative traits (*Pst*, see below). A 95% confidence interval (CI) was computed for the observed global *Fst* value using a classical cluster bootstrap procedure with 1000 iterations (Field & Welsh, 2007): CI lower and upper bounds were computed as the 95% percentiles of a theoretical distribution of 1000 *Fst* values obtained from the random sampling of the thirteen populations with replacement.

Statistical analyses

Prior to analyses, data were transformed to approximate normality: body mass, metabolic rate and excretion rate were log-transformed and boldness was square root transformed.

To evaluate the differences in trait mean across populations, we first ran an analysis of variance (ANOVA) for each trait, with the population of origin as the explicative variable. We then assessed the variability in syndromes of functional traits across populations by using path-analysis and a test of heterogeneity of covariance matrices (Cheung & Chan, 2005; Cheung, 2015). For this purpose, traits were scaled to the mean within each population (i.e. each population displays a mean of zero with a variance of one for each trait), and a general path-analysis linking each trait to the others (a saturated path analysis) was computed for each population independently using the R-package *lavaan* (Rosseel 2012). These resulted in thirteen path models (each path model corresponding to a population's syndrome), and thirteen covariance matrices that we compared using a test of heterogeneity of covariance matrices among groups (metaSEM R-package, Cheung 2015). Briefly, this analysis allows assessing the heterogeneity of covariance matrices with a combination of indices (Hooper, Coughlan, & Mullen, 2008): (i) root mean square error of approximation (RMSEA, expected to be higher than 0.06 if the matrices are heterogeneous), (ii) standardised root mean square residual (SRMR, expected to be higher than 0.09 if the matrices are heterogeneous), and (iii) comparative fit index (CFI, expected to be lower than 0.96 if the matrices are heterogeneous). Then we tested the heterogeneity among each functional trait covariation independently across populations using a test of heterogeneity (Rosenberg *et al.* 1997). We estimated and extracted the covariations between each pair of traits (six pairs in total: mass-metabolism; mass-excretion; mass-boldness; metabolism-excretion; metabolism-boldness; and excretion-boldness) from the path models described above so as to control for all relationships among traits at a time. We applied meta-analytic tools to analyse the heterogeneity in covariances. We applied the Z-Fisher transformation to each covariance value (Cov) to obtain a standardized Zr using the following formula: $Zr = 0.5\ln\frac{(1+Cov)}{(1-Cov)}$, and we calculated the corresponding standard error as: $se_{Zr} = \frac{1}{\sqrt{n-3}}$ (Nakagawa & Cuthill, 2007) where n is the sample size of the considered population. We estimated the degree of variability of *Zr* for each pair of trait among populations with a test of heterogeneity (Higgins & Thompson, 2002; Viechtbauer, 2010). This index (*H*) indicates the percentage of heterogeneity and tests whether heterogeneity in a data set is higher than that expected by chance. The standard error of *Zr* was added as a pondering parameter to the heterogeneity test to give more weight to populations with more individuals.

We assessed the determinants of trait variation and covariations between functional traits using phylogenetic models (PGLS, Garland & Ives 2000). These models allow incorporating the genetic relatedness among populations through a phylogenetic tree used to estimate a λ value corresponding to the degree of phylogenetic conservatism in the response variable. λ is expected to vary between 0 and 1, where 0 means no phylogenetic dependence in a trait among populations, and 1 means that the focal trait is phylogenetically conserved (Harvey & Purvis, 1991; Comte, Murienne, & Grenouillet, 2014). We calculated λ independently for each trait and each covariation (calculated from path analyses; see above) using only the intercept as fixed effect. Then, we used PGLS to assess the effects of temperature and predation on traits and covariations respectively. We ran PGLS for each trait and covariation (*Zr*) independently, with temperature, predation pressure (measured at the site level) and the resulting two–terms interaction as explanatory variables. The phylogenetic tree based on microsatellite markers was incorporated into each model to account for genetic relatedness among populations. When $\lambda = 0$, the model is equivalent to a classical linear model, whereas when $\lambda = 1$ it accounts for phylogenetic conservatism in trait. We then used an Information-Theoretic approach, based on AIC comparisons, to select the model(s) that best fit the data. We considered model(s) that fell within a $\Delta\text{AIC} < 4$ as 'best' model(s) as they would maximise the likelihood of the model while taking into account the number of parameters, and we rejected those with a $\Delta\text{AIC} > 4$ (Burnham & Anderson, 2002). We ran PGLS models using the *pgls* function from the R-package *caper* (Orme, 2018).

Finally, we tested whether variability in traits and covariations among populations were higher or not than expected under the hypothesis that differentiation is due to genetic drift only. We compared the *Fst* calculated on neutral genetic markers (corresponding to the level of differentiation among populations expected if genetic drift only is affecting traits) to *Pst* values calculated for each trait and covariation independently. The *Pst* is the phenotypic equivalent of the *Qst*, although calculated for wild populations when no information on the parental relatedness among individuals is available (Leinonen *et al.*, 2006). A *Pst* value higher than the global *Fst* value indicates that phenotypic differentiation among populations is higher than expected by genetic drift only, and that mechanisms such as plasticity and/or selection might explain these differences (Leinonen *et al.*, 2013). We estimated a *Pst* for each trait as: $\sigma^2_B / (\sigma^2_B + \sigma^2_W)$ where σ^2_B and σ^2_W were respectively the among- and within-population variance in the considered trait (Leinonen *et al.*, 2013). Among- and within-population variance components were estimated from generalized linear mixed models with the trait as response variable, the intercept as a fixed effect and the population as a random effect (Leinonen *et al.*, 2013). In the case of covariations, among- and within-population variance components were calculated in a similar way but with the addition of a random slope, corresponding to the co-variable trait (Appendix IV.S2). This allows estimating among- and within-population variance in the covariation between each pair of trait (Mazé-Guilmo *et al.*, 2016). The generalized linear mixed models were run using the *lme4* R-package (Bates *et al.* 2014). We applied a classical cluster bootstrap procedure with 1000 iterations (Field & Welsh, 2007) to assess the 95% confidence interval for *Pst*. We then compared the CI of *Pst* for each trait and each covariation (i.e. 10 *Pst* quantified in total: 4 single traits and 6 covariations among them) to the CI of *Fst*. All analyses were performed using R (R Core Team, 2013).

Results

Trait variability among populations

The body mass ($F = 29.859$, d.f = 12, 349, $p < 0.001$), metabolic rate ($F = 14.538$, d.f = 12, 350, $p < 0.001$), excretion rate ($F = 14.842$, d.f = 12, 322, $p < 0.001$) and boldness ($F = 5.179$, d.f = 12, 329, $p < 0.001$) were all significantly different among populations (Figure IV.3). λ was the highest for body mass ($\lambda = 0.87$) and metabolic rate ($\lambda = 0.74$), although none of these values was significantly different from zero (Table IV.1). Hence, there was no strong evidence for phylogenetic conservatism for any of the traits (see Figure IV.S1).

Table IV.1. Results of the model selection to explain the variability of functional traits and their covariations among populations. All possible phylogenetic models (PGLS, see the main text) were run for each trait and then compared based on AIC. Bold values represent models that fell in a ΔAIC < 4.

		Models				
	λ (*P*)	Null	Temperature	Predation	Temperature & Predation	Temperature -by- Predation
Mass	0.87 (0.12)	7.982	7.018	9.997	**0**	**0.194**
Metabolism	0.74 (0.19)	**0**	**1.451**	**1.997**	**2.907**	4.547
Excretion	0 (1)	**0**	**1.016**	**1.67**	**2.952**	4.521
Boldness	0.55 (1)	**0**	**1.982**	**1.932**	**3.925**	5.924
Mass-Metabolism	0 (1)	4.123	**3.528**	**1.966**	**3.929**	**0**
Mass-Excretion	0 (1)	**0**	**1.411**	**1.8**	**0.732**	**1.617**
Mass-Boldness	0 (1)	**0**	**1.93**	**1.057**	**2.559**	**2.27**
Metabolism-Excretion	0 (1)	**2.719**	4.611	4.64	5.963	**0**
Metabolism-Boldness	0 (1)	**0.35**	**1.698**	**0**	**1.757**	**3.332**
Excretion-Boldness	0 (1)	**0**	**1.102**	**1.853**	**2.862**	**3.639**

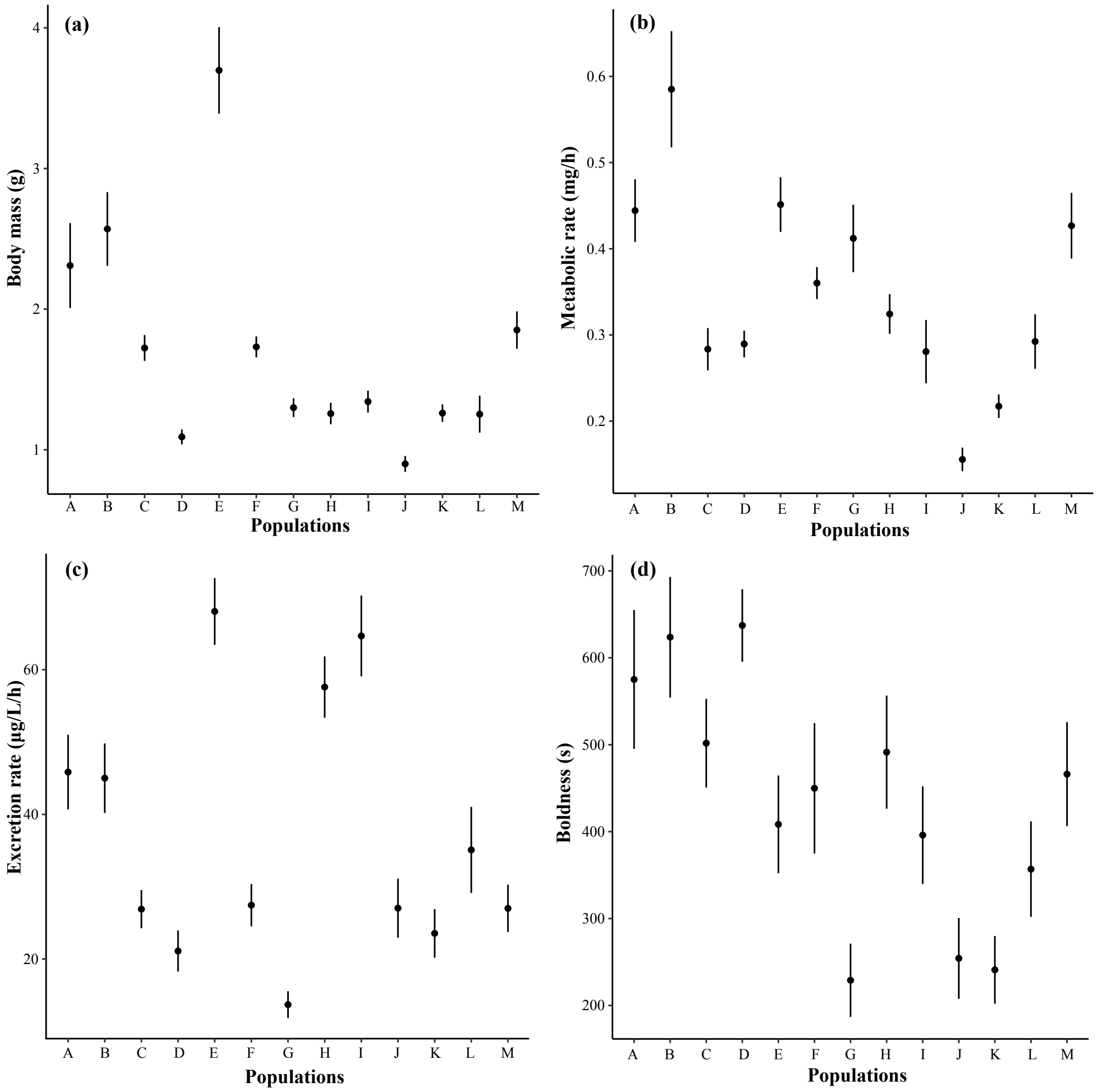


Figure IV.3. Mean trait values for body mass **(a)**, metabolic rate **(b)**, excretion rate **(c)** and boldness **(d)** in function of the population origin of fish.

Regarding determinants of trait means, the best models explaining body mass included temperature, predation pressure, and their interaction (Table IV.1). Body mass increases as temperature decreases (negative relationship) and this increase was exacerbated as predation pressure increased (Figure IV.4a). The model selection for the three other traits leads to equivalent models and the null models were, in all-three cases, the best models (Table IV.1). This suggested that metabolic rate, excretion rate and boldness were neither –or weakly-related to temperature, nor to predation pressure. Finally, the estimates of *Pst* were high for body mass, metabolic rate and excretion, and were significantly higher than the global *Fst* (Figure IV.5). Phenotypic differentiation measured for boldness was not different from what expected under the drift hypothesis.

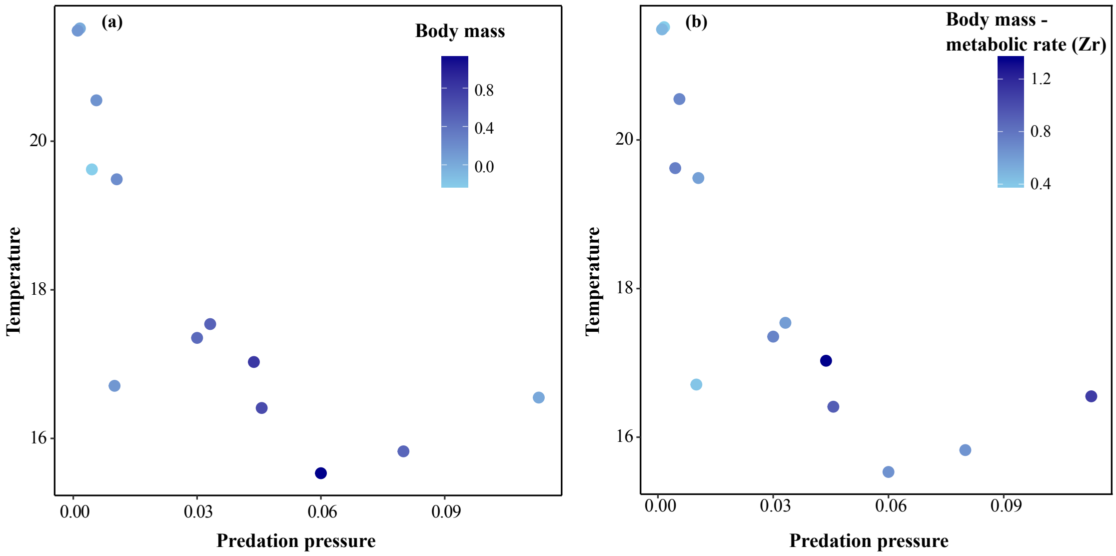


Figure IV.4. Interaction between temperature (°C) and predation pressure (ind.m^2) explains the variation in body mass **(a)**, and in the covariation between body mass and metabolic rate **(b)**.

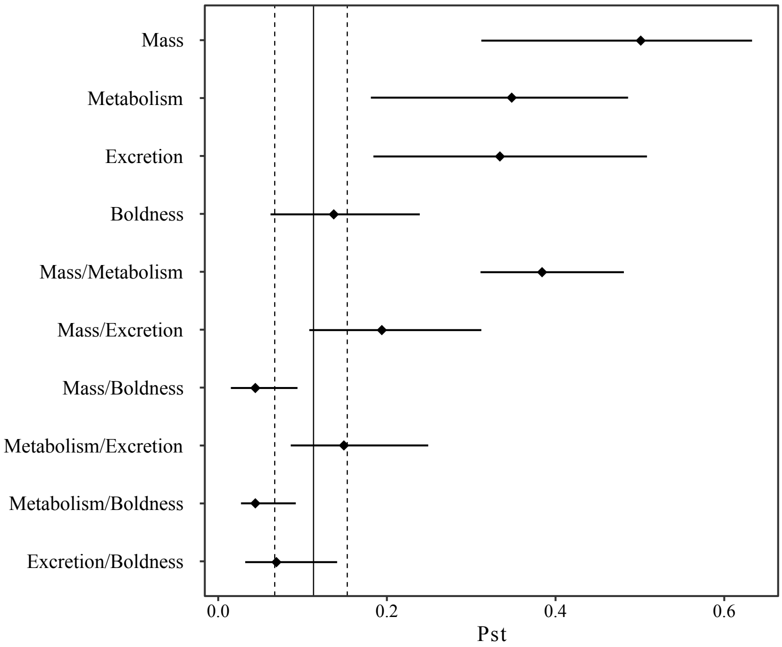


Figure IV.5. Estimates of *Pst* for each trait (body mass, metabolic rate, excretion rate and boldness) and for each covariation (body mass-metabolic rate, body mass-excretion rate, body mass-boldness, metabolic rate-excretion rate, metabolic rate-boldness and excretion rate-boldness), and *Fst* (vertical straight line) on neutral microsatellite markers. Horizontal bars represent 95% confident interval of *Pst,* and vertical dotted lines represent 95% confident interval of *Fst* that were calculated using cluster bootstrap procedure.

Among population heterogeneity in functional trait syndromes and covariations

We found that populations varied in their syndromes of functional traits since the matrices of covariations were heterogeneous (RMSEA = 0.266, CFI = 0.602, SRMR = 0.263, Figure IV.S2). For instance, the syndrome in the population F was characterised by positive covariations among body mass, metabolic and excretion rates, and a negative covariation between boldness and excretion rate (Figure IV.6a); whereas populations L displayed negative covariations between body mass and boldness, boldness and metabolic rate and metabolic and excretion rates, while the body mass-metabolic rate covariation was positive (Figure IV.6b).

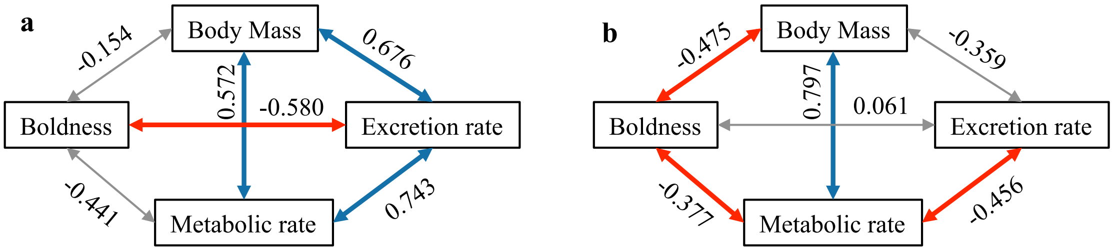


Figure IV.6. Syndromes of functional traits among populations of European minnow. Populations *F* and *L* were represented as examples in panel **(a)** and **(b)** respectively. Blue and red arrows denote significant positive and negative covariance, respectively, while the grey arrow represents non-significant covariance. Syndromes in all populations are displayed in Figure IV.S3.

This was confirmed since we also found strong significant heterogeneity among populations for several trait covariations. In particular, the covariations measured between body mass and excretion rate (H = 72.03%, Q = 45.837, d.f. = 12, $P < 0.001$), between excretion rate and metabolic rate (H = 69.20%, Q = 41.229, d.f. = 12, $P < 0.001$) and between excretion rate and boldness (H = 58.26%, Q = 31.296, d.f. = 12, P = 0.002) strongly (and significantly) varied among populations (Figure IV.7b, e and f). For instance, the covariation between metabolic and excretion rates was significantly positive for some populations, significantly negative for one population, and non-significant for the remaining populations (Figure IV.7e). The covariations between body mass and metabolic rate, between metabolic rate and boldness, and between body mass and boldness were homogeneous ($P > 0.052$, Figure IV.7a, c and d).

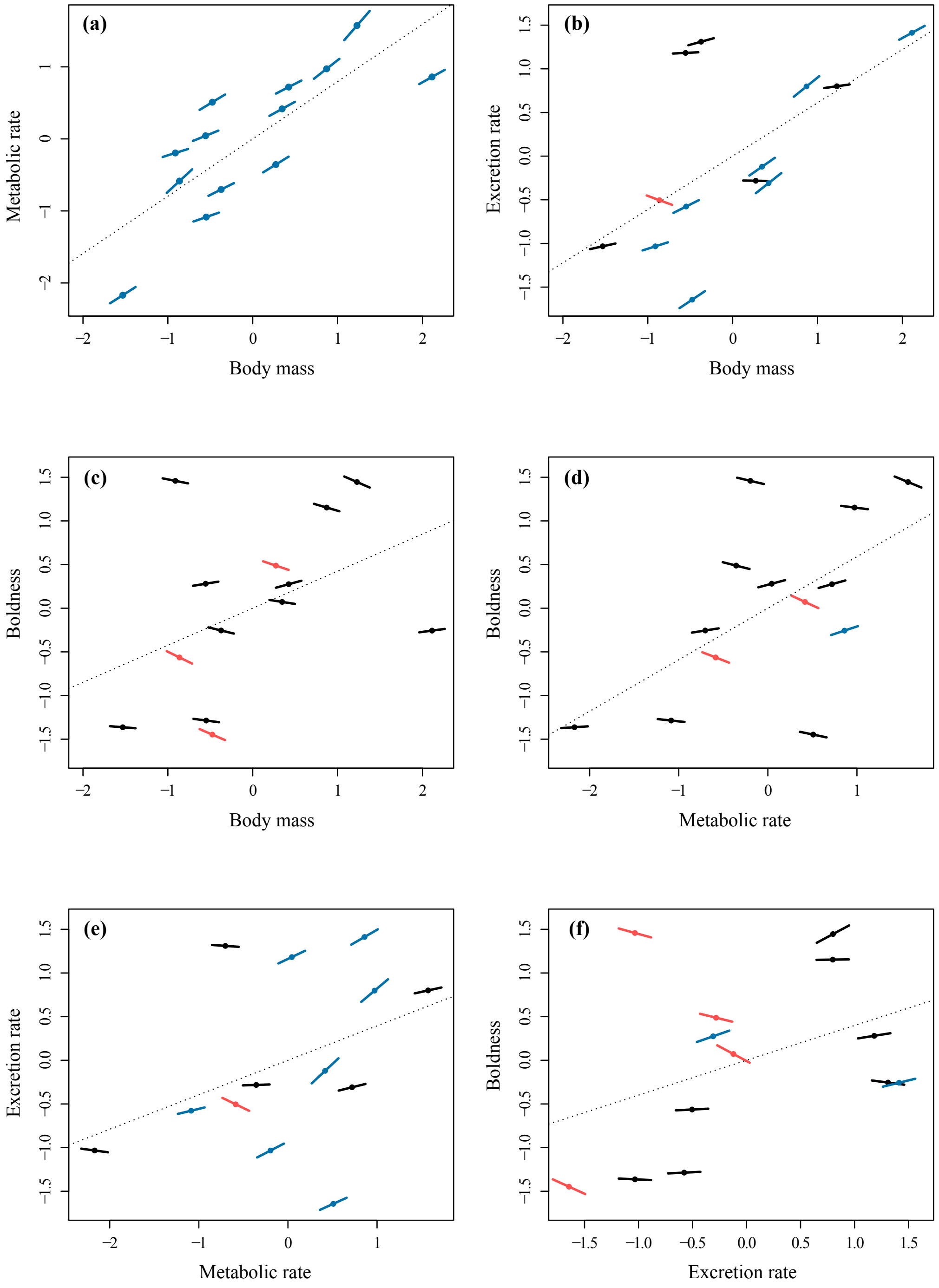


Figure IV.7. Covariations between each pair of functional traits: **(a)** body mass-metabolic rate, **(b)** body mass-excretion rate, **(c)** body mass-boldness, **(d)** metabolic rate-excretion rate, **(e)** metabolic rate-boldness and **(f)** excretion rate-boldness. Points represent the average trait value for each population, lines on points represent the covariations (i.e., the slope) between traits within each population. Blue and red lines indicate significant (α = 0.05) positive and negative covariations, respectively. The dotted lines represent the relationship between traits across the thirteen populations.

We did not find evidence for significant phylogenetic conservatism for any of the covariations (Table IV.1 and Figure IV.S3). The best models explaining the covariation between body mass and metabolic rate included temperature, predation and the temperature-by-predation interaction term (Table IV.1). For this covariation, the null model was strongly rejected from the set of the best-supported models (ΔAIC > 4), and the results suggested that the strength of the covariation tended to increase as the temperature decreases, and when the predation pressure increases (Figure IV.4b). Regarding other covariations, models including the temperature and the predation pressure were not strongly supported by the data as the null models was always selected within the set of models displaying a ΔAIC < 4 (Table IV.1).

Finally, covariation measured between body mass and metabolic rate displayed a *Pst* value that was significantly higher than the global *Fst* value (Figure IV.5). *Pst* measured for the covariation between body mass and excretion rate was higher than the global *Fst*, but the CIs of the two estimates overlapped. For other trait covariations, the *Pst* were not significantly different from the global *Fst* value (Figure IV.5).

Discussion

We demonstrated that functional traits, covariations and syndromes they form strongly varied across populations of European minnow sampled in a large riverscape, suggesting a heterogeneous "intraspecific functional space" within this riverscape. We further found that multiple processes explained variability in functional traits, their covariations, and hence in syndromes of functional traits. For instance, we found evidence for adaptive mechanisms (plasticity and/or selection) related to water temperature and/or predation for the covariation between body-mass and metabolic rate. In parallel, we found that other traits and covariations were rather driven by genetic drift, which proves that even non-adaptive processes can significantly sustain significant intraspecific variation in functional traits. Finally, we do not detect evidences of evolutionary conservatism in any of the functional traits nor in their covariations.

We showed that body mass, metabolic rate and excretion rate differed among populations more than expected by genetic drift only, suggesting trait divergences arising from selection and/or plasticity. The decrease in body mass with temperature is expected for ectotherms (Daufresne, Lengfellner, & Sommer, 2009). Here, we found a significant temperature-by-predation interaction suggesting that the effect of temperature on body mass was dependent upon the intensity of predation. We can speculate that higher body mass could allow minnows to reach a size refugee from predators, and/or to increase their locomotor performances to escape predators (Domenici, 2001; Villéger *et al.*, 2017). Nonetheless, this result should be interpreted with care since our statistical power is weak and because of collinearity between water temperature and predation. Indeed, we could alternatively argue (based on the visual inspection of bi-plot, Figure IV.S4) that a quadratic relationship (Figure IV.S4) exists between body mass and predation pressure that we may fail to properly identify because of the small sample size and the collinearity with water temperature (Prunier & Blanchet, 2018). We also found high variability in metabolic and excretion rates, which were also likely driven by adaptive mechanisms (Figure IV.5). Nonetheless, we failed in detecting the environmental pressures driving divergences in these two traits. The variability in excretion rate probably stands in trophic and stoichiometric factors, such as trophic niche, elemental composition of resources or allochtonous nutrient inputs (El-Sabaawi *et al.*, 2016; Evangelista *et al.*, 2017), which could be characteristic of each geographical site. Hence, measuring stoichiometric variability of individuals and populations would benefit to infer hypotheses regarding variability in excretion rate.

We found that not only trait can vary among populations, but also that functional traits formed different syndromes among populations of European minnow. Indeed, the sets of covariations were different among populations, and multiple patterns were identified, with some trait covariations being more robust than others. For instance, the allometric relationships between body mass and metabolic rate, and between body mass and excretion rate were both positive across all populations, but the former was homogeneous among populations (i.e. stable) whereas the later was heterogeneous and hence more flexible among populations (Figure IV.7). Similarly the covariation between excretion rate and boldness was flexible, confirming that relationships between behavioural and physiological traits can be complex (Killen *et al.*, 2013). These various functional trait covariations among populations subsequently generated variability in syndromes. Such variability has been documented in behavioural traits (Dingemanse *et al.*, 2007) and morphological traits (Berner, Stutz, & Bolnick, 2010), but rarely among multiple types of traits. The various biological mechanisms -such as pleiotropy or allometry- underlying the links among traits might therefore be modulated differently among populations, resulting in difference of syndromes (Peiman & Robinson, 2017). Hence, it would worth investigating further the biological mechanisms driving trait covariations to better appraise the variability of functional syndromes (ANNEXE 1; Killen, Atkinson, & Glazier, 2010).

Although we detected variability in syndromes of functional traits, the lack of determinants (i.e., temperature or predation) and the low *Pst* values for most trait covariations suggest that a non-negligible part in the heterogeneity in syndromes variability may –in our case- arise from the effect of genetic drift. Actually, the relationship between body mass and metabolic rate was the only covariation whose variability was likely driven by adaptive mechanisms. Indeed, as revealed by the *Pst*/*Fst* analysis and the trait-environment analysis, we found evidence that selection and/or plasticity associated to predation pressure and water temperature may drive variation observed among populations. Previous works have reported variability in the allometric relationship between body mass and metabolic rate at both the inter- and intra-specific levels in many organisms (Bokma, 2004; Glazier, 2005; Seibel, 2007). Here, covariations increase as temperature decreases and predation increases (Figure IV.4). Although this should be interpreted with care (see statistical caution above), the metabolic allometry might vary to allow individuals optimizing energetic efficiency under different environmental constraints (Glazier, 2005; Killen *et al.*, 2010). Fish can notably adapt their lifestyle to downward or upward their energetic assimilation to cope with biotic and abiotic constraints, such as predation (Killen *et al.*, 2010). This confirms that trait architecture within population can be complex, and -in some cases- allows individuals to adapt/acclimatize to their environment (Peiman & Robinson, 2017).

To conclude, we found that syndromes of functional traits can strongly vary among populations, and that both adaptive (natural selection and/or plasticity) and non-adaptive processes (genetic drift) are driving intraspecific heterogeneity in these syndromes. Since functional traits can affect ecological processes (Lavorel & Garnier, 2002; Violle *et al.*, 2007), the variability in functional syndromes may exert puzzling effects on ecological processes. For instance, the variability in covariations involving excretion rate may have implications for the dynamic of nutrient recycling and ecological stoichiometry (Vanni, 2002; Atkinson *et al.*, 2017); while in some populations large individuals should excrete a high quantity of nitrogen, they should excrete a low quantity of nitrogen for other populations, with potential consequences for primary production (McIntyre *et al.*, 2008; Evangelista *et al.*, 2017). Variability of syndromes may have further ecological effects through trophic mechanisms since individuals with different functional traits may have different trophic niche (Villéger *et al.*, 2017). Trophic variability can subsequently affect community structure and ecosystem functioning (Des Roches *et al.*, 2013). Further studies should aim at testing experimentally how heterogeneity in functional syndromes are acting on ecological dynamics.

Acknowledgements

Part I. We are grateful to the gravière team and our numerous colleagues for their help. We also thank Robby Stoks and two anonymous reviewers for their constructive and useful comments on a previous version of the manuscript. Financial support was provided by ONEMA (projects ISOLAC and ERADINVA) and by an 'ERG Marie Curie' grant (PERG08-GA-2010-276969).

Part II. We thank Kéoni Saint-Pe, Geoffrey Marselli, and other students for their helps during field works. We also thank Antoine Fargette for his help on trait measurement and animal husbandry. AR is financially supported by a Doctoral scholarship from the Université Fédérale de Toulouse. This work was undertaken at SETE, which is part of the "Laboratoire d'Excellence" (LABEX) entitled TULIP (ANR-10-LABX-41).

References

ALJANABI, S. (1997) Universal and rapid salt-extraction of high quality genomic DNA for PCR- based techniques. *Nucleic Acids Research* **25**, 4692–4693.

ARMBRUSTER, W.S. & SCHWAEGERLE, K.E. (1996) Causes of covariation of phenotypic traits among populations. *Journal of Evolutionary Biology* **9**, 261–276.

ATKINSON, C.L., CAPPS, K.A., RUGENSKI, A.T. & VANNI, M.J. (2017) Consumer-driven nutrient dynamics in freshwater ecosystems: from individuals to ecosystems. *Biological Reviews* **92**, 2003–2023.

BASSAR, R.D., BRYAN, B.L., MARSHALL, M.C., PRINGLE, C.M., REZNICK, D.N. & TRAVIS, J. (2016) Local adaptation of fish consumers alters primary production through changes in algal community composition and diversity. *Oikos*, 594–603.

BASSAR, R.D., MARSHALL, M.C., LOPEZ-SEPULCRE, A., ZANDONA, E., AUER, S.K., TRAVIS, J., PRINGLE, C.M., FLECKER, A.S., THOMAS, S.A., FRASER, D.F. & REZNICK, D.N. (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences* **107**, 3616–3621.

BATES, D., MAECHLER, M, BOLKER, B & WALKER, S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

BELL, A.M. & SIH, A. (2007) Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters* **10**, 828–834.

BERNER, D., STUTZ, W.E. & BOLNICK, D.I. (2010) Foraging trait (co)variances in stickleback evolve deterministically and do not predict trajectories of adaptive diversification. *Evolution* **64**, 2265–2277.

BESTION, E., TEYSSIER, A., AUBRET, F., CLOBERT, J. & COTE, J. (2014) Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140701–20140701.

BIRO, P.A., ADRIAENSSENS, B. & SAMPSON, P. (2014) Individual and sex-specific differences in intrinsic growth rate covary with consistent individual differences in behaviour. *Journal of Animal Ecology* **83**, 1186–1195.

BIRO, P.A., BECKMANN, C. & STAMPS, J.A. (2010) Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences* **277**, 71–77.

BOKMA, F. (2004) Evidence against universal metabolic allometry. *Functional Ecology* **18**, 184–187.

BOLNICK, D.I., AMARASEKARE, P., ARAÚJO, M.S., BÜRGER, R., LEVINE, J.M., NOVAK, M., RUDOLF, V.H., SCHREIBER, S.J. & URBAN, M.C. (2011) Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution* **26**, 183–192.

BOLNICK, D.I., SVANBÄCK, R., FORDYCE, J.A., YANG, L.H., DAVIS, J.M., HULSEY, C.D. & FORISTER, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**, 1–28.

BROMMER, J.E. (2013) On between-individual and residual (co)variances in the study of animal personality: are you willing to take the “individual gambit”? *Behavioral Ecology and Sociobiology* **67**, 1027–1032.

BROMMER, J.E. & CLASS, B. (2017) Phenotypic correlations capture between-individual correlations underlying behavioral syndromes. *Behavioral Ecology and Sociobiology* **71**.

BROWN, J.H., GILLOOLY, J.F., ALLEN, A.P., SAVAGE, V.M. & WEST, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

BURNHAM, K.P. & ANDERSON, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach.* Springer, New York.

CAPPS, K.A. & FLECKER, A.S. (2013) Invasive aquarium fish transform ecosystem nutrient dynamics. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20131520.

CHEUNG, M.W.-L. (2015) metaSEM: an R package for meta-analysis using structural equation modelling. *Frontiers in Psychology* **5**.

CHEUNG, M.W.-L. & CHAN, W. (2005) Meta-analytic structural equation modeling: A two-stage approach. *Psychological Methods* **10**, 40–64.

COLLIN, H. & FUMAGALLI, L. (2011) Evidence for morphological and adaptive genetic divergence between lake and stream habitats in European minnows (Phoxinus phoxinus, Cyprinidae). *Molecular Ecology* **20**, 4490–4502.

COLLIN, H. & FUMAGALLI, L. (2015) The role of geography and ecology in shaping repeated patterns of morphological and genetic differentiation between European minnows (*Phoxinus phoxinus*) from the Pyrenees and the Alps. *Biological Journal of the Linnean Society* **116**, 691–703.

COMTE, L., MURIENNE, J. & GRENOUILLET, G. (2014) Species traits and phylogenetic conservatism of climate-induced range shifts in stream fishes. *Nature Communications* **5**.

DARWIN, C. (1859) *On the origin of species by natural selection, or the preservation of favoured races in the struggle for life*. London John Murray.

DAUFRESNE, M., LENGFELLNER, K. & SOMMER, U. (2009) Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences* **106**, 12788–12793.

DEFOSSEZ, E., PELLISSIER, L. & RASMANN, S. (2018) The unfolding of plant growth form-defence syndromes along elevation gradients. *Ecology Letters* **21**, 609–618.

DES ROCHES, S., POST, D.M., TURLEY, N.E., BAILEY, J.K., HENDRY, A.P., KINNISON, M.T., SCHWEITZER, J.A. & PALKOVACS, E.P. (2018) The ecological importance of intraspecific variation. *Nature Ecology & Evolution* **2**, 57–64.

DES ROCHES, S., SHURIN, J.B., SCHLUTER, D. & HARMON, L.J. (2013) Ecological and evolutionary effects of stickleback on community structure. *PLoS ONE* **8**, e59644.

DÍAZ, S., PURVIS, A., CORNELISSEN, J.H.C., MACE, G.M., DONOGHUE, M.J., EWERS, R.M., JORDANO, P. & PEARSE, W.D. (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3**, 2958–2975.

DINGEMANSE, N.J., WRIGHT, J., KAZEM, A.J.N., THOMAS, D.K., HICKLING, R. & DAWNAY, N. (2007) Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology* **76**, 1128–1138.

DOMENICI, P. (2001) The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comparative Biochemistry and Physiology*, 169: 182.

EDELINE, E., LACROIX, G., DELIRE, C., POULET, N. & LEGENDRE, S. (2013) Ecological emergence of thermal clines in body size. *Global Change Biology* **19**, 3062–3068.

EL-SABAAWI, R.W., BASSAR, R.D., RAKOWSKI, C., MARSHALL, M.C., BRYAN, B.L., THOMAS, S.N., PRINGLE, C., REZNICK, D.N. & FLECKER, A.S. (2015a) Intraspecific phenotypic differences in fish affect ecosystem processes as much as bottom-up factors. *Oikos* **124**, 1181–1191.

EL-SABAAWI, R.W., MARSHALL, M.C., BASSAR, R.D., LÓPEZ-SEPULCRE, A., PALKOVACS, E.P. & DALTON, C. (2015b) Assessing the effects of guppy life history evolution on nutrient recycling: from experiments to the field. *Freshwater Biology* **60**, 590–601.

EL-SABAAWI, R.W., WARBANSKI, M.L., RUDMAN, S.M., HOVEL, R. & MATTHEWS, B. (2016) Investment in boney defensive traits alters organismal stoichiometry and excretion in fish. *Oecologia* **181**, 1209–1220.

EVANGELISTA, C., LECERF, A., BRITTON, J.R. & CUCHEROUSSET, J. (2017) Resource composition mediates the effects of intraspecific variability in nutrient recycling on ecosystem processes. *Oikos* **126**, 1439–1450.

FIELD, C.A. & WELSH, A.H. (2007) Bootstrapping clustered data. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **69**, 369–390.

FINSTAD, A.G., FORSETH, T., UGEDAL, O. & NÆSJE, T.F. (2007) Metabolic rate, behaviour and winter performance in juvenile Atlantic salmon. *Functional Ecology* **21**, 905–912.

FOURTUNE, L., PAZ-VINAS, I., LOOT, G., PRUNIER, J.G. & BLANCHET, S. (2016) Lessons from the fish: a multi-species analysis reveals common processes underlying similar species-genetic diversity correlations. *Freshwater Biology* **61**, 1830–1845.

FOURTUNE, L., PRUNIER, J.G., MATHIEU-BEGNE, E., CANTO, N., VEYSSIERE, C., LOOT, G. & BLANCHET, S. (2018) Intraspecific genetic and phenotypic diversity: parallel processes and correlated patterns?

FRIARD, O. & GAMBA, M. (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution* **7**, 1325–1330.

FROST, W.E. (1943) The natural history of the minnow, Phoxinus phoxinus. *The Journal of Animal Ecology* **12**, 139.

FRYXELL, D.C., ARNETT, H.A., APGAR, T.M., KINNISON, M.T. & PALKOVACS, E.P. (2015) Sex ratio variation shapes the ecological effects of a globally introduced freshwater fish. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20151970.

FUNK, J.L., LARSON, J.E., AMES, G.M., BUTTERFIELD, B.J., CAVENDER-BARES, J., FIRN, J., LAUGHLIN, D.C., SUTTON-GRIER, A.E., WILLIAMS, L. & WRIGHT, J. (2016) Revisiting the

Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews*.

GARLAND, T. & IVES, A.R. (2000) Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *The American Naturalist* **155**, 346–364.

GILLOOLY, J.F. (2001) Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251.

GLAZIER, D.S. (2005) Beyond the : variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews* **80**, 611.

GOLOVANOV, V.K. (2013) Ecophysiological patterns of distribution and behavior of freshwater fish in thermal gradients. *Journal of Ichthyology* **53**, 252–280.

GOUDET, J. (2005) hierfstat, a package for r to compute and test hierarchical F-statistics. *Molecular Ecology Notes* **5**, 184–186.

HARMON, L.J., MATTHEWS, B., DES ROCHES, S., CHASE, J.M., SHURIN, J.B. & SCHLUTER, D. (2009) Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* **458**, 1167–1170.

HARVEY, P.H. & PURVIS, A. (1991) Comparative methods for explaining adaptations. *Nature* **351**, 619–624.

HAWLENA, D. & SCHMITZ, O.J. (2010) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *The American Naturalist* **176**, 537–556.

HELSEN, K., ACHARYA, K.P., BRUNET, J., COUSINS, S.A.O., DECOCQ, G., HERMY, M., KOLB, A., LEMKE, I.H., LENOIR, J., PLUE, J., VERHEYEN, K., DE FRENNE, P. & GRAAE, B.J. (2017) Biotic and abiotic drivers of intraspecific trait variation within plant populations of three herbaceous plant species along a latitudinal gradient. *BMC Ecology* **17**.

HENDRY, A.P. (2016) *Eco-evolutionary dynamics.* Princeton University Press.

HIGGINS, J.P.T. & THOMPSON, S.G. (2002) Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine* **21**, 1539–1558.

HILDREW, A.G., RAFFAELLI, D. & EDMONDS-BROWNS, R. (2007) *Body size: the structure and function of aquatic ecosystems.* Cambridge University Press, Cambridge, UK.

HOOPER, D., COUGHLAN, J. & MULLEN, M.R. (2008) Structural Equation Modelling: Guidelines for Determining Model Fit. *The Electronic Journal of Business Research Methods* **6**, 8.

KEENAN, K., MCGINNITY, P., CROSS, T.F., CROZIER, W.W. & PRODÖHL, P.A. (2013) diveRsity : An R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods in Ecology and Evolution* **4**, 782–788.

KEITH, P., PERSAT, H., FEUNTEUN, E. & ALLARDI, J. (2011) *Les poissons d'eau douce de France.* Muséum National d'Histoire Naturelle and Publications Biotope. Paris and Mèze.

KETTERSON, E.D., ATWELL, J.W. & MCGLOTHLIN, J.W. (2009) Phenotypic integration and independence: Hormones, performance, and response to environmental change. *Integrative and Comparative Biology* **49**, 365–379.

KILLEN, S.S., ATKINSON, D. & GLAZIER, D.S. (2010) The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecology Letters* **13**, 184–193.

KILLEN, S.S., MARRAS, S. & MCKENZIE, D.J. (2011) Fuel, fasting, fear: routine metabolic rate and food deprivation exert synergistic effects on risk-taking in individual juvenile European sea bass. *Journal of Animal Ecology* **80**, 1024–1033.

KILLEN, S.S., MARRAS, S., METCALFE, N.B., MCKENZIE, D.J. & DOMENICI, P. (2013) Environmental stressors alter relationships between physiology and behaviour. *Trends in Ecology & Evolution* **28**, 651–658.

LANGERHANS, R.B. (2007) Evolutionary consequences of predation: avoidance, escape, reproduction, and diversification. In *Predation in Organisms* pp. 177–220. Springer Berlin Heidelberg, Berlin, Heidelberg.

LAVOREL, S. & GARNIER, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional ecology* **16**, 545–556.

LEAL, M.C., SEEHAUSEN, O. & MATTHEWS, B. (2016) The ecology and evolution of stoichiometric phenotypes. *Trends in Ecology & Evolution*.

LEINONEN, T., CANO, J.M., MÄKINEN, H. & MERILÄ, J. (2006) Contrasting patterns of body shape and neutral genetic divergence in marine and lake populations of threespine sticklebacks. *Journal of Evolutionary Biology* **19**, 1803–1812.

LEINONEN, T., MCCAIRNS, R.J.S., O'HARA, R.B. & MERILÄ, J. (2013) QST–FST comparisons: evolutionary and ecological insights from genomic heterogeneity. *Nature Reviews Genetics* **14**, 179–190.

MATTHEWS, B., DE MEESTER, L., JONES, C.G., IBELINGS, B.W., BOUMA, T.J., NUUTINEN, V., DE KOPPEL, J. VAN & ODLING-SMEE, J. (2014) Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs* **84**, 245–263.

MAZÉ-GUILMO, E., BLANCHET, S., REY, O., CANTO, N. & LOOT, G. (2016) Local adaptation drives thermal tolerance among parasite populations: a common garden experiment. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20160587.

MCINTYRE, P.B., FLECKER, A.S., VANNI, M.J., HOOD, J.M., TAYLOR, B.W. & THOMAS, S.A. (2008) Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots. *Ecology* **89**, 2335–2346.

NAKAGAWA, S. & CUTHILL, I.C. (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* **82**, 591–605.

NEI, M. (1973) Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences* **70**, 3321–3323.

ODLING-SMEE, J., LALAND, K.N. & FELDMAN, M.W. (2003) *Niche construction the neglected process in evolution.* Princeton University Press.

ORME, D. (2018) The caper package: comparative analysis of phylogenetics and evolution in R, 36.

PARADIS, E., CLAUDE, J. & STRIMMER, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290.

PAZ-VINAS, I., LOOT, G., HERMOSO, V., VEYSSIERE, C., POULET, N., GRENOUILLET, G. & BLANCHET, S. (2018) Systematic conservation planning for intraspecific genetic diversity. *Proceedings of the Royal Society B-Biological Sciences*.

PEIMAN, K.S. & ROBINSON, B.W. (2012) Diversifying and correlational selection on behavior toward conspecific and heterospecific competitors in brook stickleback (*Culaea inconstans*). *Ecology and Evolution* **2**, 2141–2154.

PEIMAN, K.S. & ROBINSON, B.W. (2017) Comparative analyses of phenotypic trait covariation within and among populations. *The American Naturalist* **190**, 451–468.

PELLETIER, F., GARANT, D. & HENDRY, A.P. (2009) Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1483–1489.

POULET, N., BEAULATON, L. & DEMBSKI, S. (2011) Time trends in fish populations in metropolitan France: insights from national monitoring data. *Journal of Fish Biology* **79**, 1436–1452.

PRUITT, J.N., RIECHERT, S.E., ITURRALDE, G., VEGA, M., FITZPATRICK, B.M. & AVILÉS, L. (2010) Population differences in behaviour are explained by shared within-population trait correlations. *Journal of Evolutionary Biology* **23**, 748–756.

PRUNIER, J.G. & BLANCHET, S. (2018) Using connectivity to identify climatic drivers of local adaptation: a response to Macdonald *et al*. *Ecology Letters* **21**, 1121–1123.

R CORE TEAM (2013) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

REALE, D., GARANT, D., HUMPHRIES, M.M., BERGERON, P., CAREAU, V. & MONTIGLIO, P.-O. (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 4051–4063.

RICE, W.R. (1989) Analyzing tables of statistical tests. *Evolution* **43**, 223.

ROFF, D.A. (1992) *The evolution of life histories. Theory and analysis*. New York, NY: Chapman & Hall.

ROUSSET, F. (2008) genepop'007: a complete re-implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources* **8**, 103–106.

ROYAUTÉ, R. & PRUITT, J.N. (2015) Varying predator personalities generates contrasting prey communities in an agroecosystem. *Ecology* **96**, 2902–2911.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013a) Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology* **94**, 1046–1056.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013b) Population structure determines functional differences among species and ecosystem processes. *Nature Communications* **4**.

SCHMITZ, O.J., HAWLENA, D. & TRUSSELL, G.C. (2010) Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13**, 1199–1209.

SEIBEL, B.A. (2007) On the depth and scale of metabolic rate variation: scaling of oxygen consumption rates and enzymatic activity in the Class Cephalopoda (Mollusca). *Journal of Experimental Biology* **210**, 1–11.

SIH, A., BELL, A. & JOHNSON, J.C. (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**, 372–378.

STEARNS, S. (1992) *The evolution of life histories*. Oxford University Press.

TORRES-DOWDALL, J., HANDELSMAN, C.A., REZNICK, D.N. & GHALAMBOR, C.K. (2012) Local adaptation and the evolution of phenotypic plasticity in trinidian guppies (*Poecilia reticulata*). *Evolution* **66**, 3432–3443.

VAN OOSTERHOUT, C., HUTCHINSON, W.F., WILLS, D.P.M. & SHIPLEY, P. (2004) micro-checker: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* **4**, 535–538.

VANNI, M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* **33**, 341–370.

VIECHTBAUER, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* **36**.

VILLÉGER, S., BROSSE, S., MOUCHET, M., MOUILLOT, D. & VANNI, M.J. (2017) Functional ecology of fish: current approaches and future challenges. *Aquatic Sciences* **79**, 783–801.

VILLÉGER, S., GRENOUILLET, G., SUC, V. & BROSSE, S. (2012) Intra- and interspecific differences in nutrient recycling by European freshwater fish. *Freshwater Biology* **57**, 2330–2341.

VIOLLE, C., ENQUIST, B.J., MCGILL, B.J., JIANG, L., ALBERT, C.H., HULSHOF, C., JUNG, V. & MESSIER, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* **27**, 244–252.

VIOLLE, C., NAVAS, M.-L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. & GARNIER, E. (2007) Let the concept of trait be functional! *Oikos* **116**, 882–892.

Wooster, D. & Sih, A. (1995) A review of the drift and activity responses of stream prey to predator presence. *Oikos* **73**, 3.

Yang, R.-C. (1998) Estimating hierarchical F -statistics. *Evolution* **52**, 950–956.

Zavorka, L., Koeck, B., Cucherousset, J., Brijs, J., Joacim Näslund, Aldvén, D., Höjesjö, J., Fleming, I.A. & Johnsson, J.I. (2017) Co-existence with non-native brook trout breaks down the integration of phenotypic traits in brown trout parr. *Functional Ecology* **31**, 1582-1591.

Supplementary information for Chapter IV.

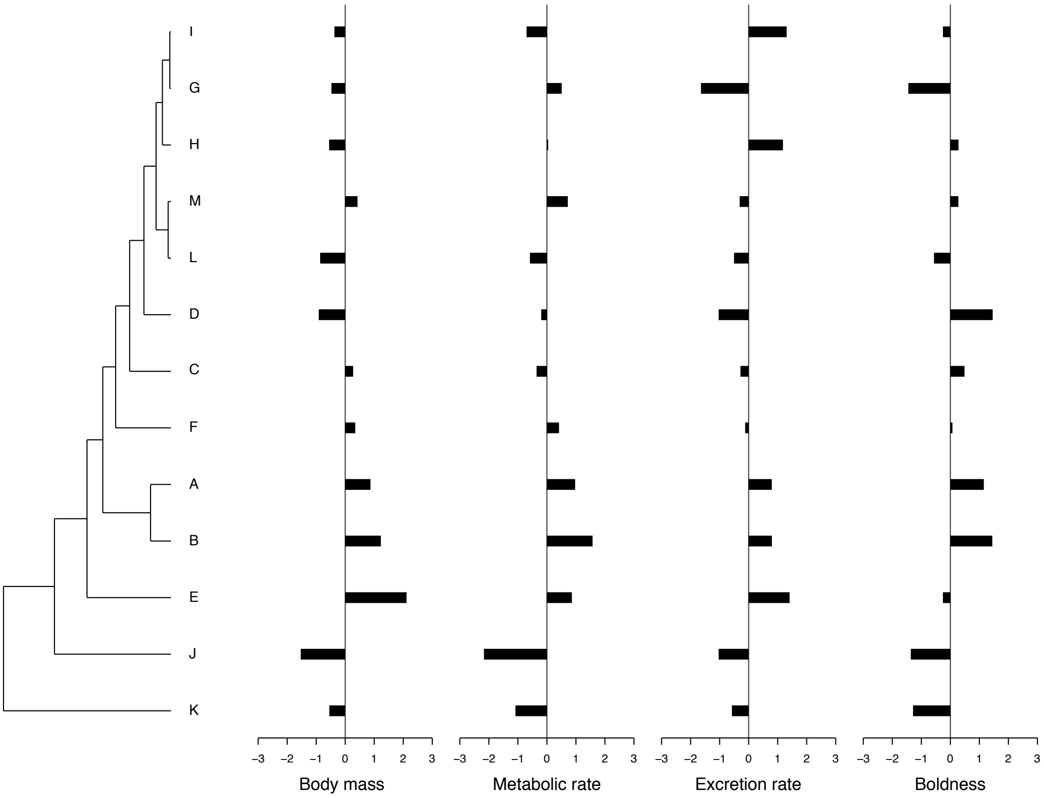


Figure IV.S1. Mean trait values (scaled to the mean) in function of the position of the populations in the phylogenetic tree constructed based on genetic distance using neutral microsatellite markers.

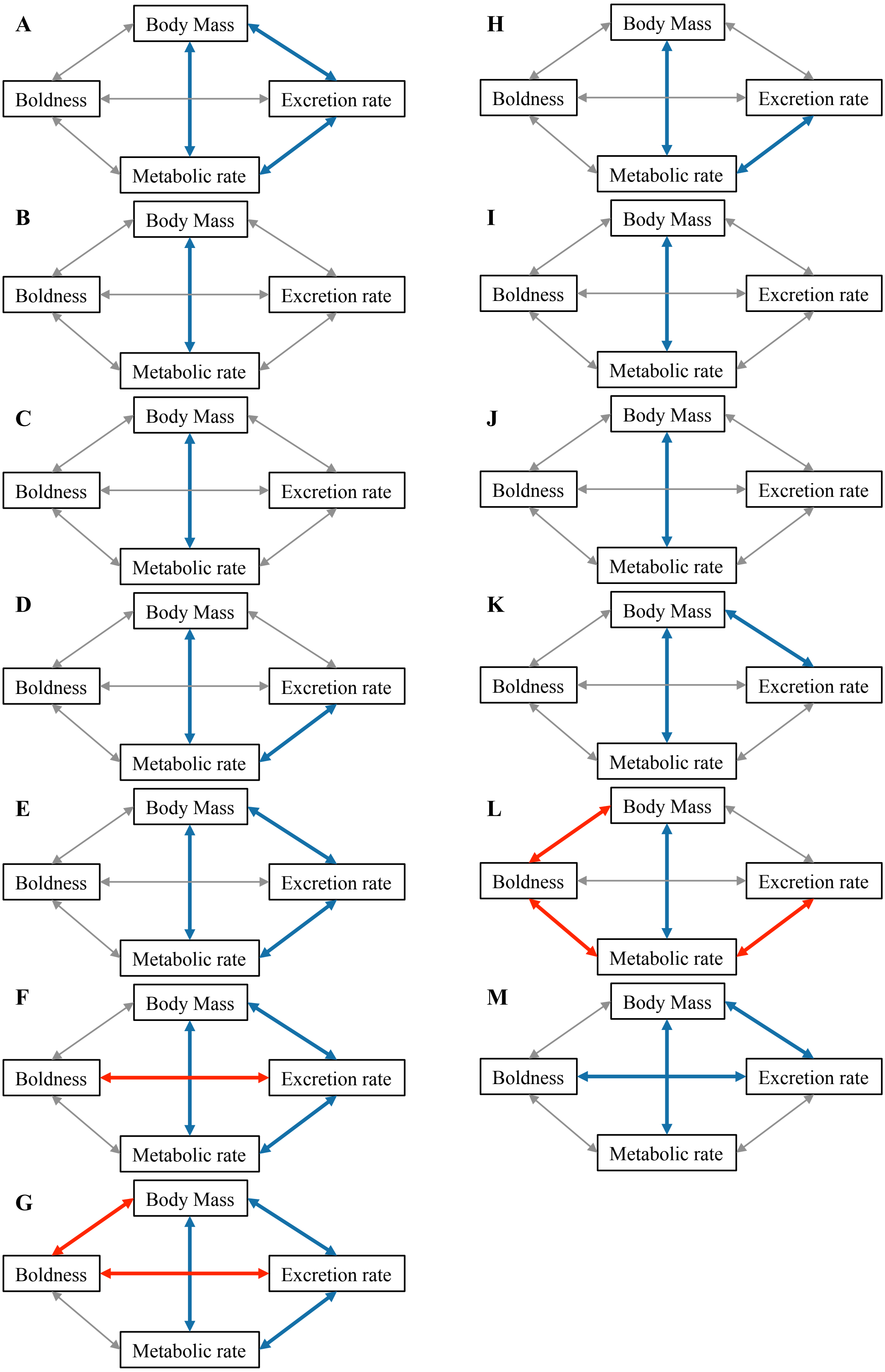


Figure IV.S2. Syndromes of functional traits in each of the 13 populations (panels A to G correspond to the populations with the same code). Blue and red arrows denote respectively significant positive and negative covariance, while the grey arrow represents non-significant covariance.

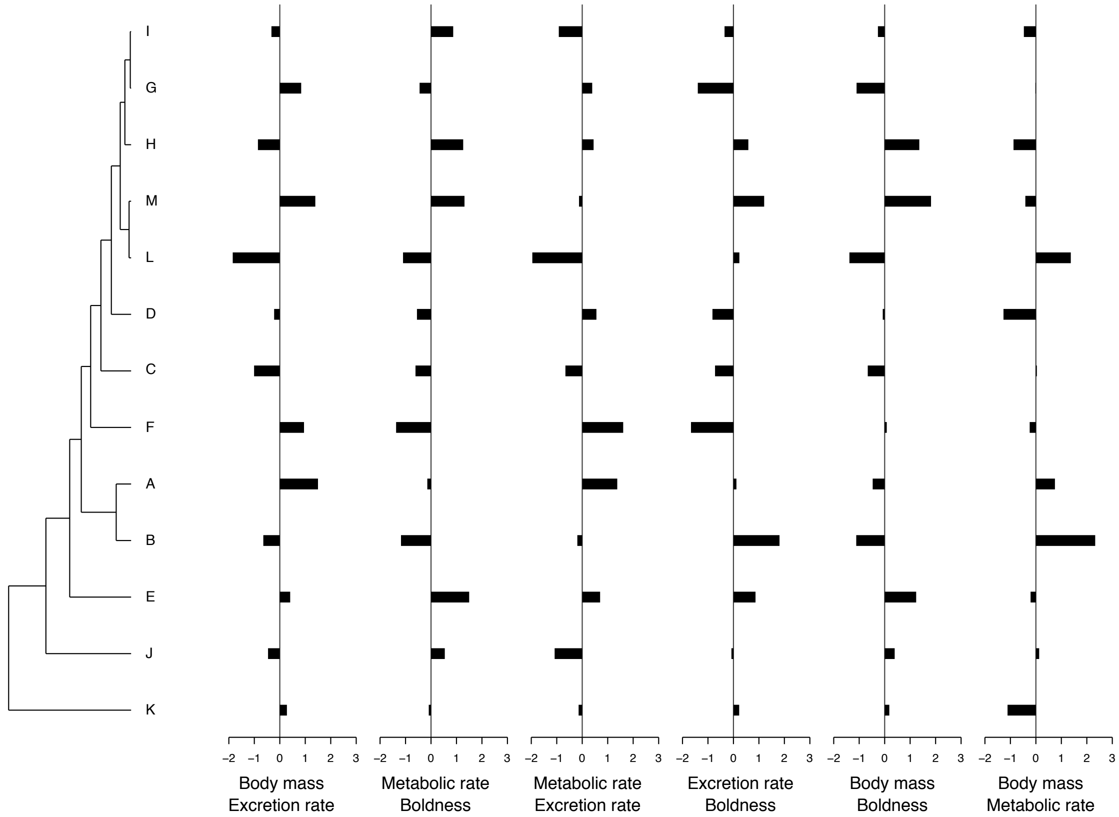


Figure IV.S3. Covariation values (transformed into a *Zr* and scaled to the mean) in function of the position of the populations in the phylogenetic tree constructed based on genetic distance using neutral microsatellite markers.

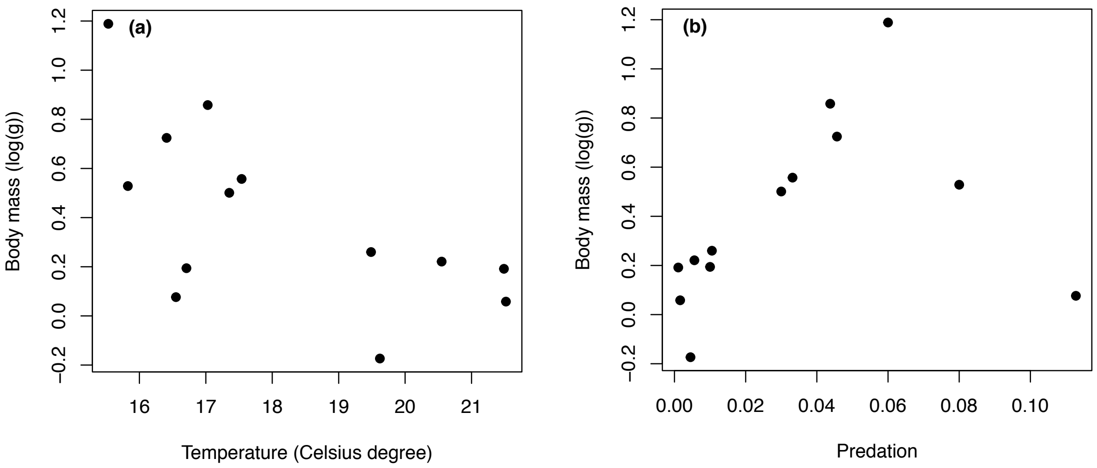


Figure IV.S4. Mean body mass (log-transformed) for each population in function of temperature **(a)** and predation pressure **(b)**.

Appendix IV.S1.

Eighteen microsatellites were amplified in two multiplex PCR as described below. Locus CtoG-075 was discarded from statistical analyses as we identified evidence for null alleles (see main text for details).

MINNOWS MULTIPLEX 1

Locus	Accession number	Reference	Allele size range	Forward primer (5 '– 3 ')
CypG9	AY439127	1	107-115	GCAGTCACGTATTAAGGCGAGCAG
Rru4	AB112740	2	163-205	TAAGCAGTGACCAGAATCCA
LleA-071	FJ601719	3	340-371	GTCTTAGATTGTGTAGCGGG
Lsou8	EF209003	4	175-200	GCGGTGAACAGGCTTAACTC
BL1-153	FJ468350	5	217-284	GCACAGCTCTAATCGGTCACT
Ppro132	AY254354	6	113-123	GCATTTCCTTTTGCTTGTAAGTCTCAA
LleB-072	FJ601720	3	150-174	TCATTAGGGAGGCTGCTTATTC
Ca3	AF277575	7	215-311	GGACAGTGAGGGACGCAGAC
CtoA-247	GU254031	8	162-182	TGCAAACATATAAACTGAAACAAGG
CtoG-075	GU254035	8	217-225	TCATTTGGATAACAATCCATCATCAC

Locus	Reverse primer (5 '– 3 ')	Fuorescent dye	Observations
CypG9	GAGCGGACTCTCAGGCACCTACC	FAM	/
Rru4	CAAAGCCTCAAAAGCACAA	FAM	/
LleA-071	ACTTCAGTTACTAAGAGATTAGTGA	FAM	/
Lsou8	TAGGAACGAAGAGCCTGTGG	HEX	/
BL1-153	TATGGTCAAACACGGGTCAA	HEX	/
Ppro132	GGTTTAACCCGATCAATGGCTGTGC	A550	/
LleB-072	CCTTTTCAACAATTTGTCACGG	A550	/
Ca3	TCTAGCCCCCAAATTTTACGG	A550	/
CtoA-247	GCAGGTATATTCCCAGCC	A565	/
CtoG-075	ACTATGTTAGCATCCACACC	A565	Null alleles

Locus	Primer mix (total 100μM each)	
	Forward (μl)	Reverse (μl)
CypG9	10	10
Rru4	16	16
LleA-071	20	20
Lsou8	6	6
BL1-153	6	6
Ppro132	20	20
LleB-072	6	6

Ca3	20	20
CtoA-247	6	6
CtoG-075	10	10

PCR MIX	**Volume (µL) X1**
H2O	3.94
Primer mix	0.06
Qiagen multiplex PCR Master Mix	5
DNA	1

Cycling conditions		
95°C	15 min	
94°C	30 s	35 cycles
56°C	90 s	35 cycles
72°C	60 s	35 cycles
60°C	45 min	
10°C	∞	

MINNOWS MULTIPLEX 2

Locus	**Accession number**	**Reference**	**Allele size range**
BL1-44	FJ468355	5	110-160
BL1-84	FJ468346	5	177-205
LleC-090	FJ601722	3	215-350
LC27	EF362792	9	104-200
LceC1	AY962241	10	93-140
MFW1	AY703054	11	163-290
Rhca20	DQ106915	5	110-130
Lsou5	EF209002	4	187-260
BL1-98	FJ468349	5	270-340

Locus	**Forward primer (5 '– 3 ')**	**Reverse primer (5 '– 3 ')**	**Fuorescent dye**	**Observations**
BL1-44	AAGACCAGCATGTGCTT	ACATAGACTAACCAGTTTCACTT	FAM	/
BL1-84	CATTACTACGGCAACCACAT	GCGAAAAGGAAAGAGACTGA	FAM	/
LleC-090	TCAGACACAACTAACCGACC	GGCGCTGTCCAGAACTGA	FAM	/
LC27	TCCAGTTCTTCCTTCCTAATT	GCGGAGGGAGAGTATGTCAA	HEX	/
LceC1	AGGTGTTGGTTCCTCCCG	TGTTATCTCGGTTTCACGAGC	A565	/
MFW1	GTCCAGACTGTCATCAGGAG	GAGGTGTACACTGAGTCACGC	A565	/
Rhca20	CTACATCTGCAAGAAAGGC	CAGTGAGGTATAAAGCAAGG	A550	/
Lsou5	CTGAAGAAGACCCTGGTTCG	CCCACATCTGCTGACTCTGAC	A550	/
BL1-98	ATTGTTTTCATTTTGTCAG	CCGAGTGTCAGAGTTATT	A550	/

Locus	Primer mix (total 100µM each)	
	Forward (µl)	Reverse (µl)
BL1-44	15	15
BL1-84	20	20
LleC-090	16	16
LC27	10	10
LceC1	40	40
MFW1	60	60
Rhca20	6	6
Lsou5	40	40
BL1-98	60	30

PCR MIX	Volume (µL) X1
H2O	3.867
Primer mix	0.133
Qiagen multiplex PCR Master Mix	5
DNA	1

References for appendix IV.S1

1 Baerwald, M. R., & May, B. (2004). Characterization of microsatellite loci for five members of the minnow family Cyprinidae found in the Sacramento-San Joaquin Delta and its tributaries. Molecular Ecology Notes, 4(3), 385–390. doi:10.1111/j.1471-8286.2004.00661.x

2 Barinova, A., Yadrenkina, E., Nakajima, M., & Taniguchi, N. (2004). Identification and characterization of microsatellite DNA markers developed in ide Leuciscus idus and Siberian roach Rutilus rutilus. Molecular Ecology Notes, 4(1), 86–88. doi:10.1046/j.1471-8286.2003.00577.x

3 Dubut, V., Martin, J.-F., Gilles, A., Van Houdt, J. K. J., Chappaz, R., & Costedoat, C. (2009). Isolation and characterization of polymorphic microsatellite loci for the dace complex: Leuciscus leuciscus (Teleostei: Cyprinidae). Molecular Ecology Resources, 9(4):1179-83. doi: 10.1111/j.1755-0998.2009.02594.x

4 Muenzel, F. M., Sanetra, M., Salzburger, W., & Meyer, A. (2007). Microsatellites from the vairone Leuciscus souffia (Pisces: Cyprinidae) and their application to closely related species. Molecular Ecology Notes, 7(6), 1048–1050. doi:10.1111/j.1471-8286.2007.01772.x

5 Dubut, V., Martin, J.-F., Costedoat, C., Chappaz, R., & Gilles, A. (2009). Isolation and characterization of polymorphic microsatellite loci in the freshwater fishes Telestes souffia and Telestes muticellus (Teleostei: Cyprinidae). Molecular Ecology Resources, 9(3), 999–1001. doi:10.1111/j.1755-0998.2009.02536.x

6 Bessert, M. L., & Orti, G. (2003). Microsatellite loci for paternity analysis in the fathead minnow, Pimephales promelas (Teleostei: Cyprinidae). Molecular Ecology Notes, 3(4), 532–534. doi:10.1046/j.1471-8286.2003.00501.x

7 Dimsoski, P., Toth, G. P., & Bagley, M. J. (2000). Microsatellite characterization in central stoneroller Campostoma anomalum (Pisces : Cyprinidae). Molecular Ecology, 9(12), 2187–2189.

8 Dubut, V., Sinama, M., Martin, J.-F., Meglécz, E., Fernandez, J., Chappaz, R., … Costedoat, C. (2010). Cross-species amplification of 41 microsatellites in European cyprinids: A tool for evolutionary, population genetics and hybridization studies. BMC Research Notes, 3(1), 135. doi:10.1186/1756-0500-3-135

9 VyskočIlová, M., šImková, A., & Martin, J.-F. (2007). Isolation and characterization of microsatellites in Leuciscus cephalus (Cypriniformes, Cyprinidae) and cross-species amplification within the family Cyprinidae. Molecular Ecology Notes, 7(6), 1150–1154. doi:10.1111/j.1471-8286.2007.01813.x

10 Larno, V., Launey, S., Devaux, A., & Laroche, J. (2005). Isolation and characterization of microsatellite loci from chub Leuciscus cephalus (Pisces: Cyprinidae). Molecular Ecology Notes, 5(4), 752–754. doi:10.1111/j.1471-8286.2005.01052.x

11 Crooijmans, R. P. M. A., Poel, J. J. V. der, Groenen, M. A. M., Bierbooms, V. A. F., & Komen, J. (1997). Microsatellite markers in common carp (Cyprinus carpio L.). Animal Genetics, 28(2), 129–134. doi:10.1111/j.1365-2052.1997.00097.x

Appendix IV.S2. Construction of the linear mixed effects models (LMM) used to calculated *Pst* of covariations. *Pst* were calculated as: σ^2_{Bs} / (σ^2_{tot}) where σ^2_{Bs} is the among variation in the slope and σ^2_{tot} is the total amount of variance (Mazé-Guilmo *et al.*, 2016). Traits were scaled to the mean. LMM were run using the lme4 package in R (Bates *et al.* 2014).

Y	*X*	Random effect	Random slope
Metabolic rate	Intercept	Population	Body mass
Excretion rate	Intercept	Population	Body mass
Excretion rate	Intercept	Population	Metabolic rate
Excretion rate	Intercept	Population	Boldness
Boldness	Intercept	Population	Body mass
Boldness	Intercept	Population	Metabolic rate

References for appendix IV.S2

Bates, D., Maechler, M, Bolker, B & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Mazé-Guilmo, E., Blanchet, S., Rey, O., Canto, N. & Loot, G. (2016). Local adaptation drives thermal tolerance among parasite populations: a common garden experiment. *Proc. R. Soc. B Biol. Sci.*, 283, 20160587.

Chapitre V.

Linking intraspecific variability in trophic niche and functional niche along an environmental gradient

Allan Raffard[1, 2], Frédéric Santoul[2], Simon Blanchet[1, 3], & Julien Cucherousset[3]

[1] *CNRS, Université Toulouse III Paul Sabatier, Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UMR-5321, F-09200 Moulis, France.*

[2] *EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France.*

[3] *Laboratoire Évolution et Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, IRD, UPS, 118 route de Narbonne, Toulouse 31062, France.*

Manuscript in preparation.

Résumé

Historiquement, la variabilité trophique des organismes a été étudiée afin de comprendre les règles d'assemblage et la coexistence des espèces au sein des communautés. Cependant, la variabilité trophique au niveau intraspécifique peut aussi jouer un rôle clé en déterminant la valeur sélective des individus et en affectant le fonctionnement des écosystèmes. Plusieurs facteurs conditionnent la variabilité trophique. Les traits fonctionnels (en particulier les traits morpho-anatomiques) peuvent notamment contraindre la niche trophique des organismes. Il a été récemment proposé que les conditions environnementales puissent également être essentielles puisqu'elles modulent les ressources disponibles et les traits fonctionnels. Ainsi, cette étude s'est intéressée à la quantification de la variabilité trophique entre douze populations de vairons (*Phoxinus phoxinus*) le long d'un gradient environnemental (température, largeur de rivière, occupation des sols et altitude). A l'aide d'une analyse des isotopes stables ($\delta^{13}C$ et $\delta^{15}N$), nous avons défini la niche trophique de chaque population puis exploré les déterminants fonctionnels et environnementaux de (i) la position trophique et de l'origine des ressources utilisées, (ii) la taille de la niche trophique et (iii) la similarité trophique entre les populations. Nous avons montré que la position trophique et l'origine des ressources utilisées étaient associées aux traits fonctionnels relatifs à la taille et aux performances locomotrices des individus, et que ces relations pouvaient être dépendantes des conditions environnementales. Les populations avaient des niches trophiques de différentes tailles, mais nous n'avons pas trouvé les déterminants sous-jacents. Finalement, la similarité trophique entre populations était corrélée à la similarité environnementale mais pas à leur similarité fonctionnelle. Ces résultats confirment que la variabilité trophique est régie par des interactions complexes entre les traits fonctionnels des individus et les conditions environnementales dans lesquelles ils vivent. La niche trophique régissant les interactions entre différents niveaux trophiques, il serait intéressant d'évaluer les effets de la variabilité trophique entre populations d'une même espèce sur les communautés de proies et le fonctionnement des écosystèmes.

Abstract

Trophic niche variability has been primarily investigated to explain species coexistence and community assembly. Intraspecific trophic variability is nonetheless important, as it drives individual fitness and their impacts ecosystem functioning. This variability depends upon multiple factors, notably functional traits (morpho-anatomical traits) can mechanistically constrain trophic niche. It has also been suggested that environmental conditions play an important role in shaping both resource availability and functional traits. Here, we quantified intraspecific variability in the trophic niche among twelve populations of European minnow (*Phoxinus phoxinus*) distributed along a gradient of environmental conditions (water temperature, river width, land use, altitude and canopy cover). Using stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$), we aimed to identify the functional and environmental determinants of (i) the trophic position and the origin of resource use, (ii) trophic niche size, and (iii) trophic similarity among populations. Results demonstrated that the trophic position and the origin of resource use were associated to functional traits (mainly related to individual size and locomotion performance). Environmental conditions also played an important role by shaping directly trophic niche and by modulating the relationships between stable isotopes and functional niches. The trophic niche size was also different among populations, although no determinant was identified here. Finally, trophic similarity among populations was correlated to environmental similarity but not to the functional similarity among populations. This study suggests that the determinants of intraspecific variability in trophic niche are complex, context-dependent and related to the interactions among functional traits and environmental conditions. Since trophic niche determines the interactions among trophic levels in a food web, it might be worth investigating further the effects of trophic variability among populations on prey community structure and ecosystem functioning.

Introduction

The integration of resource exploitation by organisms in community ecology has a longstanding history, and has been used to understand the relationships among species that allow them to coexist, notably through niche variation (Tilman, 1982). Trophic variability has also been demonstrated to be a key facet in intraspecific variability (Van Valen, 1965; Bolnick *et al.*, 2003; Araújo, Bolnick, & Layman, 2011). Trophic variability does not only allow populations to face environmental variability (e.g. consumption of alternative resource in harsh environmental conditions), but it is also an essential mechanisms by which intraspecific variability affects communities and ecosystems (Bolnick *et al.*, 2003). Indeed, variability in consumer diet can result into differences in the density or behaviour of their preys, which can then cascade on lower trophic levels (Chapter III; Terborgh & Estes, 2010; Des Roches *et al.*, 2018). For instance, individual three-spined sticklebacks (*Gasterosteus aculeatus*) foraging on distinct prey items such as benthic or limnetic invertebrates can lead to different prey community composition that subsequently affect, through trophic cascade, ecosystem functioning (Harmon *et al.*, 2009). Therefore, quantifying intraspecific trophic niche variability in wild populations and determining its determinants is needed to understand how organisms adapt to, and affect their surrounding environment.

Trophic variability can be driven by several factors related to individual phenotypes and the environmental conditions that individuals are facing (Schluter, 1995; Araújo *et al.*, 2011). For instance, resource polymorphism is a widespread phenomenon whereby individuals within population display strong phenotypic differences (e.g. body shape, mouth size) that are associated with distinct trophic niches (Skulason & Smith, 1995; Smith & Skulason, 1996). Amongst the phenotypic traits that can be important for resource acquisition, the functional traits of individuals are commonly used by ecologists to indirectly infer the trophic niche of species (Villéger *et al.*, 2017). Functional traits are defined as the individual characteristics that respond to environmental variations, and that represent its ecological role in the environment (so-called functional response and effect traits, respectively, Violle *et al.*, 2007; Díaz *et al.*, 2013). Functional traits are related to the potential trophic niches of organisms because they govern the abilities of organisms to detect and to acquire resources (i.e., morphology, Sibbing & Nagelkerke, 2001; Villéger *et al.*, 2010; Zhao *et al.*, 2014). It has been primarily assumed that individual morphology, resource acquisition ability and trophic niche were strongly linked. For instance, the mouth shape of fish (and other gap-limited consumers that shallow their prey) is strongly associated with the size of food item they consumed, which consequently affect their trophic position (Karpouzi & Stergiou, 2003). The relationship between functional traits and trophic variability has been primarily investigated at the interspecific level, and studies at the intraspecific level are still scarce (but see Vrede *et al.*, 2011; Cucherousset *et al.*, 2011; Zhao *et al.*, 2014).

In addition, environmental conditions are important drivers of individual trophic niche (Rosenblatt & Schmitz, 2016; Zandonà *et al.*, 2017). Environmental conditions can induce strong pressures on individuals that shape their trophic niche, either by modifying their metabolic needs (e.g. temperature) or by modulating resources availability (e.g. competition within and between species) (Cucherousset *et al.*, 2007; Hawlena & Schmitz, 2010; Boersma *et al.*, 2016). Effects of environmental conditions could, however, be complex and context-dependent because functional traits are facing and responding to environmental pressures (Díaz *et al.*, 2013). Hence, at the community level, communities displaying similar functional traits might be trophically dissimilar because environmental conditions differ and imposes different constraints on communities (Pool *et al.*, 2016). However, our knowledge on the determinants of trophic variability at the population level is extremely limited despite the fact it could help predicting the ecological effects of intraspecific variability.

Here, we investigated the functional and environmental determinants of trophic niche variability among populations using the European minnow (*Phoxinus phoxinus*) as a model organism. We used stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) to assess trophic niche of 12 populations distributed along a gradient of environmental conditions. We focused on an environmental gradient that included water temperature, river width, altitude, canopy cover and land use, and that was likely to affect the phenotype and the trophic niche of organisms. For instance, temperature can affect the organism physiological needs (Rosenblatt & Schmitz, 2016), river width is related to habitat size and resource heterogeneity, and the canopy cover of river is linked to the allochtonous inputs (Bartels *et al.*, 2012; Evangelista *et al.*, 2014). This study had three objectives related to three different facets of trophic characteristics of populations, i.e (i) the trophic position and the origin of resource use, (ii) trophic niche size (i.e., alpha-diversity approach), and (iii) trophic niche similarity among populations (i.e., beta-diversity approach). We first assessed the effects of environmental factors and functional traits on trophic position and origin of resource use. We expected that the mean trophic position may depend upon the ability (e.g. mouth shape) of individuals to consume larger prey (Carroll, 2004). Second, we tested the relationship between trophic niche size and functional niche size and environmental conditions and tested the hypothesis that populations with a high functional niche size (richness) also display a high trophic richness (Pool *et al.*, 2016). Finally, we quantified the association between trophic, functional and environmental similarity. We tested the prediction that populations facing similar environmental conditions and that are functionally similar should display similar trophic niches.

Material and methods

Model species and study sites

This study focused on the European minnow (*Phoxinus phoxinus*) as a model species. This Cyprinid fish live in relatively cold water, including streams, temperate rivers and mountain lakes (Frost, 1943; Keith *et al.*, 2011). European minnows from different populations and inhabiting in distinct environments have been reported to display a high level of phenotypic and genetic differentiation, suggesting the existence of an adaptation to environmental conditions (Collin & Fumagalli, 2015). As a generalist species, European minnow is omnivorous and feed on small invertebrates, zooplankton and even on filamentous algae and plant debris (Frost, 1943; Collin & Fumagalli, 2011).

European minnows were collected by electrofishing (DK 7000) in 12 rivers located in the Garonne basin in southwestern of France (Figure V.1). Rivers were selected based on *a priori* knowledge of their environmental characteristics to maximise the level of variability between populations. In June 2016, we sampled approximately 100 adult minnows in each river along a ~200m long river stretch to ensure representativeness of habitat heterogeneity. Twenty to twenty-seven individuals were randomly collected from the pool of individuals for further analyses to obtain a representative sample of each population. Electrofishing was performed under authorizations of local authorities. Fish were euthanized in the field using an overdose of anaesthetic (benzocaine: 25 mg.L^{-1}) and subsequently frozen at -20°C until further analyses. Overall, a total of 305 individuals (mean number of individuals/populations ± standard error (SE) = 25.41 ± 0.63, min = 20, max = 27) were subsequently used in the analyses. In addition, we sampled benthic invertebrates in each stretch at three different locations using Surber nets to correct fish stable isotope values for between-river comparisons of the stable isotope niche (Post *et al.*, 2007; Jackson & Britton, 2014). Ephemeroptera from the Heptageniidae and Baetis families were used here.

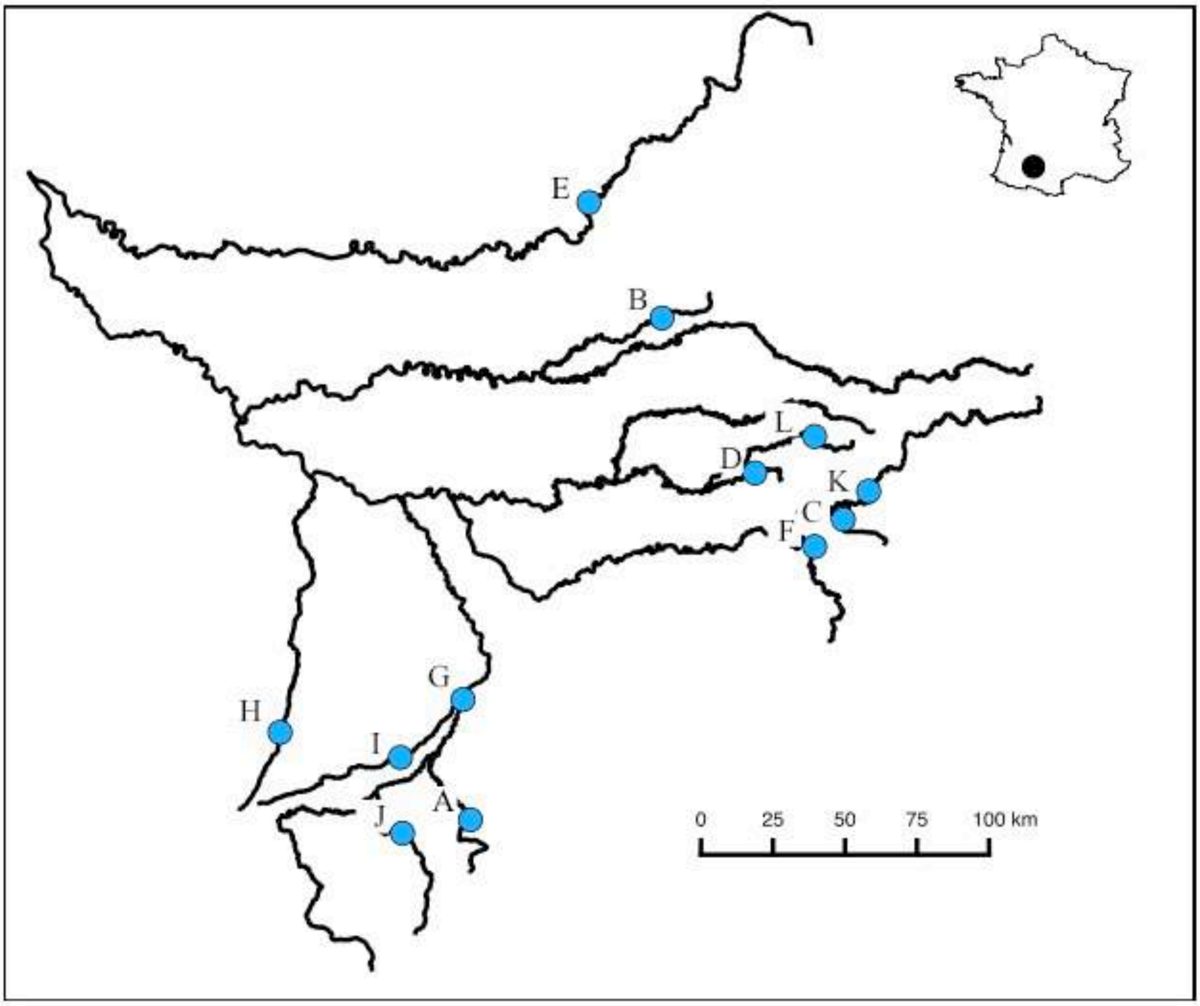


Figure V.1. Spatial distribution of the 12 studied populations (A to L) in the Garonne basin.

In each river stretch, five environmental variables were measured. These included water temperature, river width, altitude, canopy cover and land use (i.e. urban, forest, agricultural). Water temperature was recorded daily from July to September 2017 using automatic sensors (HOBO, one measurement every hour). River width was measured five times along each stretch, and these five measurements were then averaged. Canopy cover was assessed visually using a score ranging from 1 to 5; 1 indicating a low canopy cover (0% to 25%) and 5 a high canopy cover (75% to 100%). The altitude was recorded from existing maps (www.geoportail.gouv.fr). Finally, land use was quantified as the percentage of urban, forest or opened agricultural land in a 500 m diameter area around the sampling stretch. Land use was obtained from the 'Corine Land Cover' database (National Institute of Geographical Information). Since the environmental variables were correlated, they were summarized using a principal component analysis (PCA, ade4 package in R, Chessel, Dufour, & Dray, 2007; R

Core Team, 2013). We selected the two main axes of the PCA that explained 75% of the total variance of the seven variables. The first axis (54% of the variance explained, hereafter referred to as *upstream-downstream gradient*) was correlated to temperature (loading value = 0.84), width (0.84), altitude (-0.68), canopy cover (-0.81), urban (0.80) and agricultural cover (-0.74), while the second axis (21%, hereafter referred to as *forest cover*) was correlated to the percentage of forest cover in the land use (-0.96) (Figure V.2).

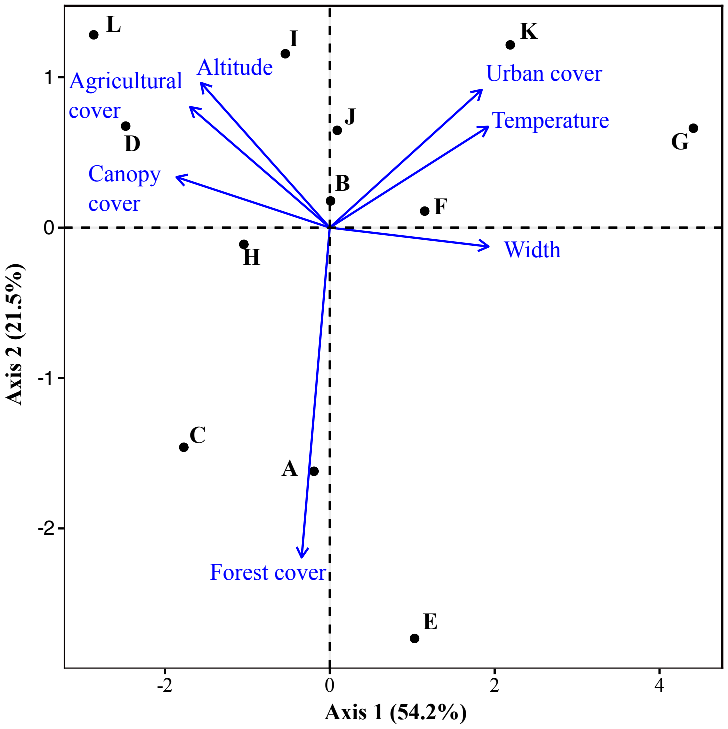


Figure V.2. Two principal component axes describing environmental variability among the 12 studied sites.

Functional niche

In March 2017, fish were unfrozen and weighed for body mass (*M*) to the nearest 0.001 g. Then, a set of 15 morpho-anatomical measurements were taken for each individuals (Zhao *et al.*, 2014). These measurements included mouth depth (*Md*), mouth width (*Mw*) and body width (*Bw*) measured to the nearest 0.01 mm using a digital calliper. Fish were pictured from the side and additional measurements obtained through picture analysis using the software ImageJ: body length (*Bl*), body depth (*Bd*), body depth at the level of pectoral fin insertion (*PFd*), mouth distance from the bottom of the head (*Mo*), head depth (*Hd*), eye diameter (*Ed*), distance between the center of the eye and the bottom of the head (*Eh*), caudal peduncle minimal depth (*CPd*), caudal fin depth (*CFd*), pectoral fin length (*PFl*), distance between the insertion of the pectoral fin to the bottom of the body (*PFi*). Finally, gut length (*Gl*) was measured following dissection. The 15 morpho-anatomical measurements were then used to calculate 10 morphological ratios (Table V.S1) describing functional traits of fish (Villéger *et al.*, 2010; Zhao *et al.*, 2014).

The functional space was then calculated by analysing the 10 morphological traits and body mass using a PCA. Three axes explaining up to 51% of the total variance in the functional traits were then used for subsequent analyses (Table V.1). The *functional axis 1* (24% of the variance explained) was associated with individual body mass (loading = 0.87), the oral gape surface (-0.58) and the body transversal shape (-0.83) (Table V.1). The *functional axis 2* (14%) was mostly related to the position of the pectoral fin, the hydrodynamism, and to eye size of individuals (Table V.1), describing the detection and locomotion capacity of individuals. The *functional axis 3* (13%) was mostly correlated to the position of the mouth and the eye, and described to the position of the fish in the water column (Table V.1); highest values on this axis described most benthic individuals.

Stable isotope niche

We used stable isotope analyses to infer the trophic niche of each population. A sample of dorsal muscle was collected on each individual, oven-dried at 60°C for 48h and analysed for stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) at the Cornell Isotope Laboratory (COIL, Ithaca, NY).

To allow between-river comparison of the stable isotope niche, stable isotope values were corrected for each population using the $\delta^{15}N$ and $\delta^{13}C$ values of invertebrates (Ephemeroptera including Baetis and Heptagenidae) following (Olsson *et al.*, 2009; Jackson & Britton, 2014). Therefore, the trophic position (TP) of each individual was calculated as:

$$TP = \frac{\delta^{15}N_i - \delta^{15}N_{base}}{3.4} + 2$$

where $\delta^{15}N_i$ was the $\delta^{15}N$ value of each individual, $\delta^{15}N_{base}$ was the mean $\delta^{15}N$ of baseline invertebrates, 3.4 the fractionation factor between trophic level and 2 was the trophic position of baseline invertebrates (Post *et al.*, 2007).

Then, we corrected the δ^{13}C to describe the origin of resource use (*ORU*) with the following equation:

$$ORU = \frac{\delta^{13}C_i - \delta^{13}C_{meaninv}}{CR_{inv}}$$

where $\delta^{13}C_i$ was the δ^{13}C value for each individual fish, $\delta^{13}C_{meaninv}$ was the average δ^{13}C value of baseline invertebrates (i.e., Baetis and Heptagenidae), and CR_{inv} was the range of δ^{13}C values occupied by invertebrates calculated as $\delta^{13}C_{max}$ - $\delta^{13}C_{min.}$

Table V.1. Loading values of the functional traits on each of the three selected principal component axes. Bold values represent variables that contribute more than 10% to the axes construction.

Functional traits	Axis 1 (24%)	Axis 2 (14%)	Axis 3 (13%)
Body mass	**0.87**	0.25	0.08
Oral gape surface	**-0.58**	0.10	**-0.46**
Oral gape shape	0.16	**0.47**	**-0.44**
Oral gape position	0.36	-0.06	**-0.61**
Gut length	0.28	-0.01	-0.02
Eye size	-0.16	**-0.64**	-0.01
Eye position	0.49	**-0.45**	**-0.56**
Body transversal shape	-0.40	**0.43**	**-0.42**
Body transversal surface	**-0.83**	-0.31	0.01
Pectoral fin position	0.21	**-0.54**	-0.31
Caudal peduncle throttling	0.45	-0.15	0.29

Statistical analyses

We first tested for differences in trophic and functional niches among populations using a multiple analysis of variance with permutations (PERMANOVA) on the stable isotope variables (trophic position and origin of resource use), and on the three functional axes

(Anderson, 2001). Analyses were performed using the *adonis* function from the *vegan* package in R (Oksanen *et al.*, 2005).

We then tested the effect of the environment and functional axes on the trophic position and the origin of resource use using linear mixed effect models (package *lme4* in R, (Bates *et al.*, 2014). Trophic position and origin of resource use were set as dependent variables, while the two environmental axes (upstream-downstream gradient and forest cover), the three functional axes and the resulting two-term interactions between environmental and functional axes were set as fixed effects. Population identity was set as a random effect. A model selection procedure using the Akaike Information Criteria (AIC) was performed, and all models that felt within a ΔAIC < 14 were then used in a model averaging procedure (Burnham, Anderson, & Huyvaert, 2011; Symonds & Moussalli, 2011). This allowed to calculate the mean coefficient (i.e. slope) associated with each explicative variable along with the sum of the Akaike weight (Σw) of the models in which the target variable appears, which indicates the probability of the explicative variable to be a component of the best model (Burnham & Anderson, 2002; Symonds & Moussalli, 2011).

To identify the determinant of the trophic niche size of populations (i.e., alpha-diversity), we calculated the stable isotope richness by measuring the convex-hull area of all individuals in each population (Layman *et al.,* 2007). First, trophic position and origin of resource use values were scaled between 0 and 1 to give the same weight to both variable when computing stable isotope richness (Cucherousset & Villéger, 2015). Second, we calculated stable isotope richness on 1000 bootstraps using a subsample of 15 individuals in each population (corresponding to 75% of all individuals in the population with the lower number of individuals analysed for stable isotopes) to avoid potential bias due to differences in sample sizes among populations. We calculated the median value and 95% confident interval (CI) from the 1000 bootstraps for each population. The same approach was used to calculate the functional richness using the three functional axes. The association between stable isotope richness, functional richness and environmental conditions were tested using bivariate linear models with stable isotope richness used as a dependent variable and functional richness or the environmental conditions (upstream-downstream gradient and forest cover) as explicative variables.

Finally, we investigated the determinants of the trophic and functional similarity (i.e. beta-diversity). To do so, stable isotope similarity was quantified by calculating Euclidean distance between centroids of each pair of populations (Pool *et al.*, 2016). Centroids were calculated as the mean trophic position and origin of resource use for each population (Schmidt, Harvey, & Vander Zanden, 2011). Functional similarity was calculated using the same approach on the three functional traits axes. Environmental similarity among river stretches was assessed by calculating the Euclidean distance on the two environmental axes. Lastly, we calculated the riparian distance (i.e. through the river network) among populations as we can expect that geographically close populations display similar trophic and functional niches. The associations between stable isotope beta-diversity and functional beta-diversity, environmental dissimilarity and riparian distance were tested using multiple regression on distance matrices (Lichstein, 2007) (package *ecodist* in R, Goslee & Urban, 2007). Stable isotope beta-diversity was set as dependent variable and functional beta-diversity, environmental dissimilarity and hydrographical distance were set as explicative variables. Then, we assessed whether functional beta-diversity was explained by environmental dissimilarity and hydrographical distance.

Results

Overall, there was a significant difference in the trophic niche of the studied populations (PERMANOVA, $p < 0.001$). Specifically, trophic position varied from 2.55 (± 0.02 SE) to 3.59 (± 0.02) and the origin of resource use varied from -1.53 (± 0.08) to 0.70 (± 0.06) among populations (Figure V.3a). Functional traits were also significantly different among populations (PERMANOVA, $p < 0.001$, Figure V.3b).

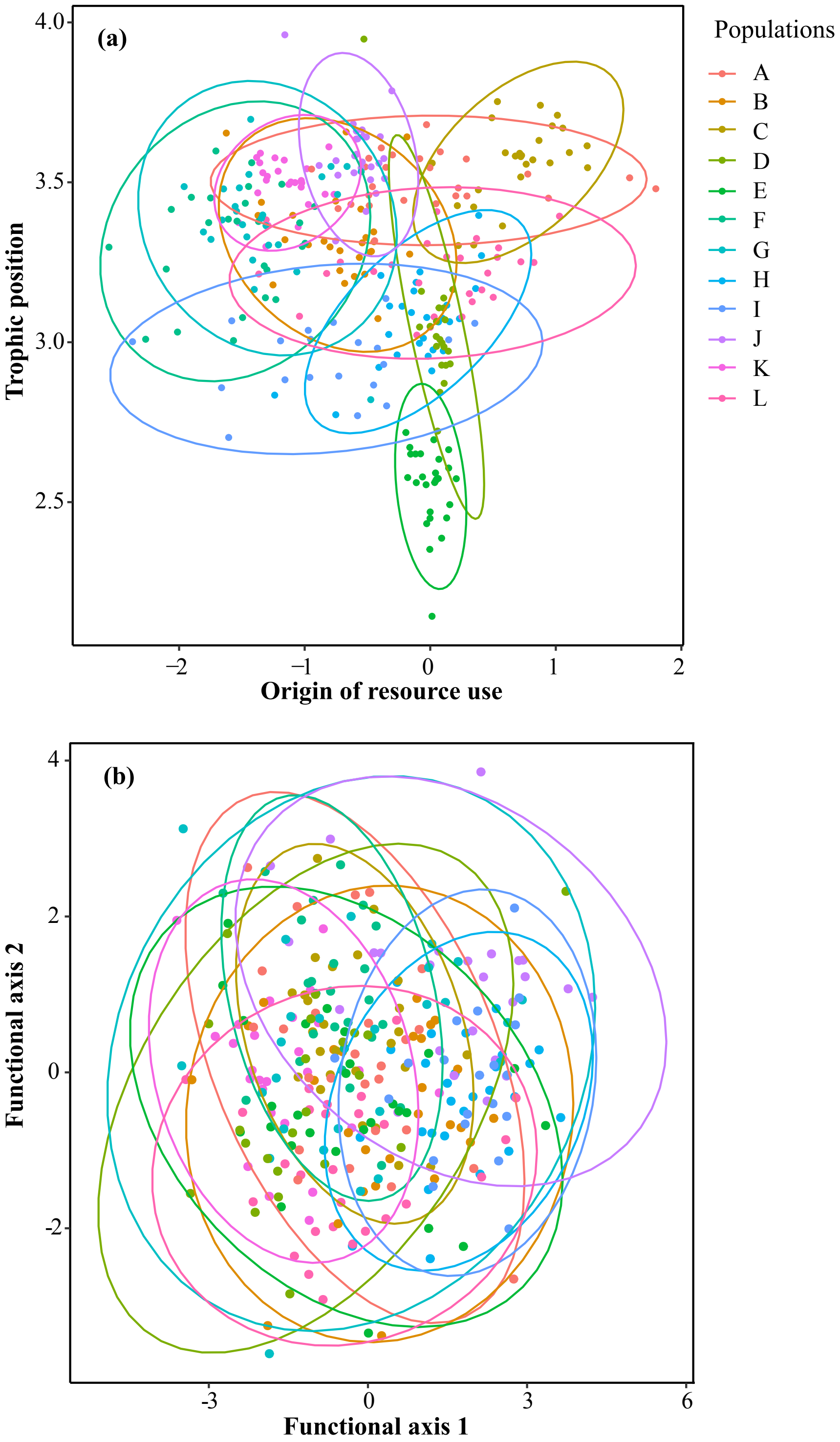


Figure V.3. Distribution of each individual from the 12 studied populations in the **(a)** trophic (trophic position and origin of resource use) and **(b)** functional (PC axes 1 and 2) spaces.

The trophic position of individual was likely affected by the interaction between the functional axis 2 and the upstream-downstream gradient axis (Σw > 0.98). The trophic position was also affected, to a lesser extent, by the functional axes 1 and 3, and the forest cover axis (Σw > 0.70, Table V.2). The negative relationship between trophic position and functional axes 1suggested that larger individuals displayed a lower trophic position (Figure V.4a). Increased values in functional axis 2 were associated with an increased trophic position that was dependent of the upstream-downstream gradient axis (Figure V.4b). The origin of resource use was related to the functional axis 2 (Table V.2, Figure V.4c), to the upstream-downstream gradient axis (Figure V.4d), and to the interaction between upstream-downstream gradient and functional axis 1 (Table V.2, Figure V.S1).

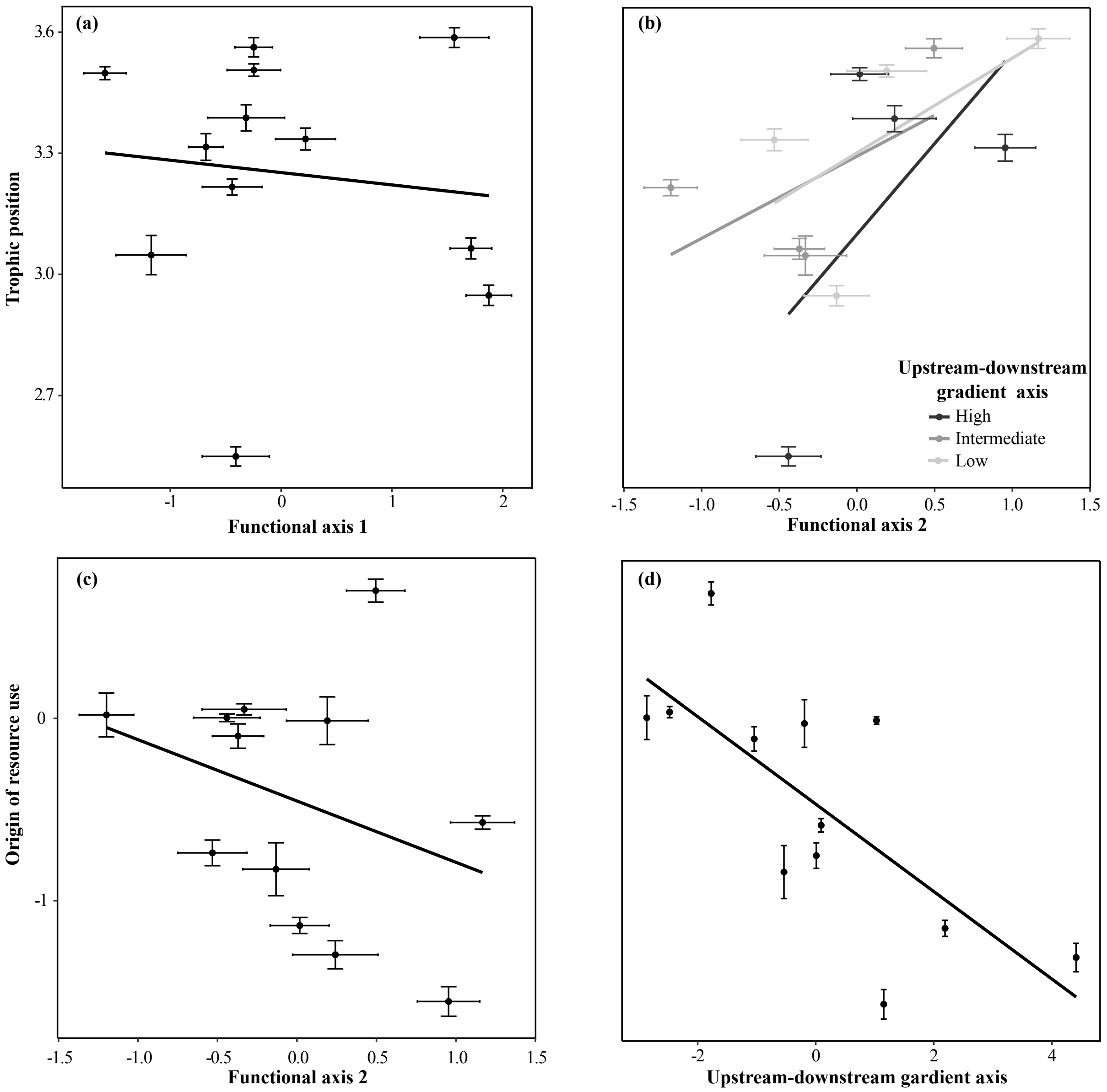


Figure V.4. Relationships **(a)** between functional axis 1 and trophic position, **(b)** among functional axis 2, upstream-downstream gradient axis and the trophic position, **(c)** between functional axis 2 and the origin of resource use, and **(d)** between upstream-downstream gradient axis and the origin of resource use. Error bars represent ± 1 SE.

Table V.2. Results of the model averaging procedure used to determine the best predictors of stable isotope values (TP: trophic position, ORU: origin of resource use). Σ*w* represents the sum of the Akaike weight and β is the averaged estimate of variables over models in which the variables appeared. Environmental axis 1: upstream-downstream gradient; Environmental axis 2: forest cover.

	TP		ORU	
	Σ*w*	β	Σ*w*	β
Functional axis 1	**0.79**	**-0.011**	**0.95**	**-0.019**
Functional axis 2	**0.99**	**-0.005**	**0.9**	**-0.047**
Functional axis 3	**0.71**	**-0.006**	0.39	-0.246
Environmental axis 1	**0.99**	**0.021**	**1.00**	**-0.270**
Environmental axis 2	**0.79**	**0.062**	**0.99**	**-0.021**
Functional axis 1 x Environmental axis 1	0.18	0.013	**0.85**	**-0.024**
Functional axis 1 x Environmental axis 2	0.2	0.016	0.56	-0.013
Functional axis 2 x Environmental axis 1	**0.98**	**0.006**	0.37	-0.011
Functional axis 2 x Environmental axis 2	0.15	0.002	0.24	-0.0002
Functional axis 3 x Environmental axis 1	0.14	0.002	0.12	0.012
Functional axis 3 x Environmental axis 2	0.55	0.001	0.07	-0.004

Stable isotope richness was highly variable among populations and varied from 0.011 [95% confident interval (CI) = 0.007 - 0.015] to 0.073 (CI = 0.051 - 0.088) among populations (Figures V.2 and V.S2). Similarly, populations were variable in their functional richness that varied from 0.014 (CI = 0.008 - 0.021) to 0.062 (CI = 0.036 - 0.093) (Figures V.2 and V.S2). There was no significant relationship between stable isotope richness and functional niche size (F = 0.107, d.f = 1, 10, p = 0.749) or environmental conditions (F = 0.062, d.f = 1, 10, p = 0.807 and F = 1.665, d.f = 1, 10, p = 0.225 for upstream-downstream gradient and forest cover, respectively). In addition, there was no significant relationship between functional richness and environmental conditions (F = 0.652, d.f = 1, 10, p = 0.476 and F = 0.200, d.f = 1, 10, p = 0.664, for upstream-downstream gradient and forest cover, respectively).

Stable isotope beta-diversity was positively related to environmental dissimilarity (R^2 = 0.157, p = 0.009, Table V.3), indicating that populations experiencing similar environmental conditions displayed more similar trophic niches (Figure V.5a). However, stable isotope beta-diversity was neither related to functional beta-diversity (R^2 = 0.022, p = 0.233) nor to geographical distance (R^2 = 0.001, p = 0.789) (Table V.3, Figure V.5b). Functional beta-diversity was neither related to hydrographical distance nor to environmental dissimilarity (Table V.3).

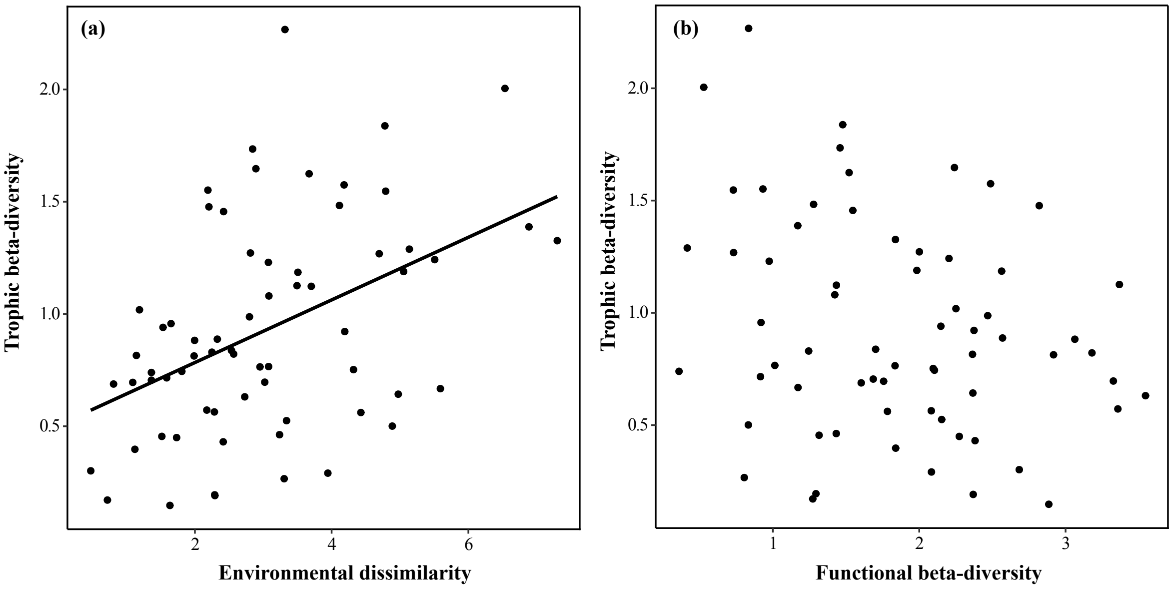


Figure V.5. Relationships between **(a)** environmental dissimilarity and trophic (stable isotope) beta-diversity, and between **(b)** functional and trophic beta-diversity.

Table V.3. Results of the multiple regressions on distance matrices to determine the predictors of trophic (stable isotope) and functional beta-diversity. R^2 of the full model (with all variable included) and associated p-values are given as indication. Significant p-values are displayed in bold.

	Trophic beta-diversity			Functional beta-diversity		
	Estimate	R^2	*P*	Estimate	R^2	*P*
Full model	-	0.223	**0.023**	-	0.059	0.396
Functional beta-diversity	-0.009	0.022	0.233	-	-	-
Environmental dissimilarity	0.128	0.157	**0.009**	-0.124	0.057	0.158
Hydrographical distance	< 0.001	0.001	0.789	< 0.001	0.001	0.833

Discussion

The present study reveals the existence of a strong level of trophic and functional niches variability across twelve populations of European minnow distributed along an environmental gradient. We further showed that trophic position and the origin of resource use were linked with functional traits associated to individual size and their locomotion performance. Environmental conditions also played an important role in these relationships by shaping directly trophic niche or by modulating the relationships between trophic and functional traits. This was further confirmed by the fact that trophic similarity among populations was most likely due to environmental similarity among sites rather than functional similarity among populations. Finally, trophic niche size was also different among populations, although no potential determinant was detected here.

Our results confirms previous studies suggesting that biotic pressures, such as predation and competition, can induce shift in individual stable isotope niche by modifying resource availability (Cucherousset *et al.*, 2007; Zandonà *et al.*, 2017). Indeed, the environmental gradient studied here, that included water temperature, river width and land use (i.e. roughly describing an upstream-downstream gradient), was negatively related to the origin of resource used by individuals. While we cannot assess the precise diet of fish in our study, visual inspection of the data (Figures V.S3 and V.S4) suggests that individuals in downstream parts of the river network derived their energy mostly on the detritus chain (i.e., lower value of $\delta^{13}C$, Vannote *et al.*, 1980), while individuals in the upstream parts of the river network derived their energy mostly from the periphyton-based food chain. In parallel, river characteristics also affected the trophic niche of European minnow populations by shaping the relationship with functional traits. Indeed, although the trophic position of individuals was associated to their capacity to detect and capture prey (i.e., the functional axis 2 was notably correlated with eye size), this relationship was conditioned upon the environment. In fact, it was actually stronger in the downstream parts of the river networks (Figure V.4b). This is possibly because large downstream rivers may be more turbid due to an accumulation of detritic organic matter (Vannote *et al.*, 1980), affecting the foraging behaviour of fish (Bonner & Wilde, 2002; Shoup & Wahl, 2009). Therefore, larger eye size could provide an advantage for foraging on invertebrates in highly turbid rivers. These results suggest that intraspecific variability in trophic niche probably stands in complex interactions among functional traits and environmental conditions.

The strong dependency of trophic niche upon environmental conditions is further supported by the fact that trophic similarity among populations was correlated to environmental similarity. In a recent review paper Villéger *et al.* (2017) argued that functional traits determined fundamental niche, which was then narrowed into a smaller realized trophic niche because the environment modulates the prey availability. In line with that claim, our results showed that despite potential links between stable isotope niche and functional traits taken individually, when we investigated the trophic and functional beta-diversity (an approach that allows accounting for the overall trophic and functional niche) functionally similar populations did not have similar trophic niche. This confirms previous results at the community level (Pool *et al.*, 2016), and suggests that individuals may therefore display some degree of trophic variability in regard with their functional niche causing a mismatch between trophic and functional niche (Bellwood *et al.*, 2006). This potential trophic variability was probably driven by environmental characteristics that govern ecological opportunities and resource availability (Brandl, Hoey, & Bellwood, 2014; Evangelista *et al.*, 2014).

Ecological opportunities within rivers, which describe notably the diversity of available resources, may be worth to investigate when studying the trophic niche size of populations (Araújo *et al.*, 2011). We indeed found variability in trophic niche size among the twelve populations but that was neither associated with the environmental characteristics of the rivers nor with the functional niche size. The ecological opportunities, habitats or available resources within a river might shape the number of ecological niche available for individuals fish and *in fine* the population trophic niche size (Vrede *et al.*, 2011; Evangelista *et al.*, 2014). Measuring this information may therefore increase prediction capacities regarding the trophic niche size of populations (Bolnick *et al.*, 2003). Surprisingly - and contrary to expectations (Pool *et al.*, 2016) -, the functional niche size was not related to trophic niche size. Alternatively, determinants of trophic niche size may stand in other intra-population phenotypic components. Ontogeny, physiological, behavioural and life history traits might all be essential in determining the energetic needs of individuals and subsequently their diet (Zhao *et al.*, 2014; Pool *et al.*, 2016; Rosenblatt & Schmitz, 2016). Overall, measuring additional parameters, such as the age structure of populations, life-history traits of fish and microhabitat characteristics, should help to infer mechanisms regarding the variability of trophic niche size.

Trophic niche is central for organism performance in their environment as it is tightly linked to individual fitness (Cucherousset *et al.*, 2011). Additionally, variability in trophic niche is primordial for predicting the effect of intraspecific diversity on ecosystem functioning (Harmon *et al.*, 2009). While trophic niche could be mechanistically related to specific functional traits (e.g., body size or prey detection capacity), environmental characteristics (e.g., temperature, river width) are important as they modify the relationships between function and diet. Environmental conditions can even encompass functional traits constrains as similar river hosted populations with similar trophic niche but not functional niche. Our results confirm that morpho-anatomical traits are not trivially linked to the trophic niche (Bellwood *et al.*, 2006; Pool *et al.*, 2016; Villéger *et al.*, 2017), and reinforce the needs to further investigate the trophic niche variability within species to better appraise intraspecific effects on ecosystems.

Acknowledgements.

We thank Kéoni Saint-Pe for help during fieldwork. We also thank Lucie Di Gesu and Alix Hervé for their helps in functional trait measurement and data acquisition. AR is financially supported by a Doctoral scholarship from the Université Fédérale de Toulouse. This work was undertaken at SETE, EDB and Ecolab. SETE and EDB are part of the 'Laboratoire d'Excellence' (LABEX) entitled TULIP (ANR-10-LABX-41).

References

ANDERSON, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral ecology* **26**, 32–46.

ARAÚJO, M.S., BOLNICK, D.I. & LAYMAN, C.A. (2011) The ecological causes of individual specialisation. *Ecology Letters* **14**, 948–958.

BARTELS, P., CUCHEROUSSET, J., STEGER, K., EKLÖV, P., TRANVIK, L.J. & HILLEBRAND, H. (2012) Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* **93**, 1173–1182.

BATES, D., MAECHLER, M, BOLKER, B & WALKER, S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

BELLWOOD, D.R., WAINWRIGHT, P.C., FULTON, C.J. & HOEY, A.S. (2006) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B: Biological Sciences* **273**, 101–107.

BOERSMA, M., MATHEW, K.A., NIEHOFF, B., SCHOO, K.L., FRANCO-SANTOS, R.M. & MEUNIER, C.L. (2016) Temperature driven changes in the diet preference of omnivorous copepods: no more meat when it's hot? *Ecology Letters* **19**, 45–53.

BOLNICK, D.I., SVANBÄCK, R., FORDYCE, J.A., YANG, L.H., DAVIS, J.M., HULSEY, C.D. & FORISTER, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**, 1–28.

BONNER, T.H. & WILDE, G.R. (2002) Effects of turbidity on prey consumption by prairie stream fishes. *Transactions of the American Fisheries Society* **131**, 1203–1208.

BRANDL, S.J., HOEY, A.S. & BELLWOOD, D.R. (2014) Micro-topography mediates interactions between corals, algae, and herbivorous fishes on coral reefs. *Coral Reefs* **33**, 421–430.

BURNHAM, K.P. & ANDERSON, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach.* Springer, New York.

BURNHAM, K.P., ANDERSON, D.R. & HUYVAERT, K.P. (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* **65**, 23–35.

CARROLL, A.M. (2004) Morphology predicts suction feeding performance in centrarchid fishes. *Journal of Experimental Biology* **207**, 3873–3881.

CHESSEL, D., DUFOUR, A.B. & DRAY, S. (2007) ade4: Analysis of ecological data: exploratory and euclidean methods in multivariate data analysis and graphical display. R package version, 1–4.

COLLIN, H. & FUMAGALLI, L. (2011) Evidence for morphological and adaptive genetic divergence between lake and stream habitats in European minnows (*Phoxinus phoxinus*, Cyprinidae). *Molecular Ecology* **20**, 4490–4502.

COLLIN, H. & FUMAGALLI, L. (2015) The role of geography and ecology in shaping repeated patterns of morphological and genetic differentiation between European minnows (*Phoxinus phoxinus*) from the Pyrenees and the Alps. *Biological Journal of the Linnean Society* **116**, 691–703.

CUCHEROUSSET, J., ACOU, A., BLANCHET, S., BRITTON, J.R., BEAUMONT, W.R.C. & GOZLAN, R.E. (2011) Fitness consequences of individual specialisation in resource use and trophic morphology in European eels. *Oecologia* **167**, 75–84.

CUCHEROUSSET, J., AYMES, J.C., SANTOUL, F. & CÉRÉGHINO, R. (2007) Stable isotope evidence of trophic interactions between introduced brook trout *Salvelinus fontinalis* and native brown trout *Salmo trutta* in a mountain stream of south-west France. *Journal of Fish Biology* **71**, 210–223.

CUCHEROUSSET, J. & VILLÉGER, S. (2015) Quantifying the multiple facets of isotopic diversity: New metrics for stable isotope ecology. *Ecological Indicators* **56**, 152–160.

DES ROCHES, S., POST, D.M., TURLEY, N.E., BAILEY, J.K., HENDRY, A.P., KINNISON, M.T., SCHWEITZER, J.A. & PALKOVACS, E.P. (2018) The ecological importance of intraspecific variation. *Nature Ecology & Evolution* **2**, 57–64.

DÍAZ, S., PURVIS, A., CORNELISSEN, J.H.C., MACE, G.M., DONOGHUE, M.J., EWERS, R.M., JORDANO, P. & PEARSE, W.D. (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3**, 2958–2975.

EVANGELISTA, C., BOICHE, A., LECERF, A. & CUCHEROUSSET, J. (2014) Ecological opportunities and intraspecific competition alter trophic niche specialization in an opportunistic stream predator. *Journal of Animal Ecology* **83**, 1025–1034.

FROST, W.E. (1943) The natural history of the minnow, *Phoxinus phoxinus*. *The Journal of Animal Ecology* **12**, 139.

GOSLEE, S.C. & URBAN, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* **22**.

HARMON, L.J., MATTHEWS, B., DES ROCHES, S., CHASE, J.M., SHURIN, J.B. & SCHLUTER, D. (2009) Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* **458**, 1167–1170.

HAWLENA, D. & SCHMITZ, O.J. (2010) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *The American Naturalist* **176**, 537–556.

JACKSON, M.C. & BRITTON, J.R. (2014) Divergence in the trophic niche of sympatric freshwater invaders. *Biological Invasions* **16**, 1095–1103.

KARPOUZI, V.S. & STERGIOU, K.I. (2003) The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology* **62**, 1353–1365.

KEITH, P., PERSAT, H., FEUNTEUN, E. & ALLARDI, J. (2011) *Les poissons d'eau douce de France.* Muséum National d'Histoire Naturelle and Publications Biotope. Paris and Mèze.

LAYMAN, C.A., ARRINGTON, D.A., MONTAÑA, C.G. & POST, D.M. (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* **88**, 42–48.

LICHSTEIN, J.W. (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology* **188**, 117–131.

OKSANEN, J., KINDT, R., LEGENDRE, P. & O'HARA, R.B. (2005) vegan: community ecology package. Version 1.7–81.

OLSSON, K., STENROTH, P., NYSTRÖM, P. & GRANÉLI, W. (2009) Invasions and niche width: does niche width of an introduced crayfish differ from a native crayfish? *Freshwater Biology* **54**, 1731–1740.

POOL, T.K., CUCHEROUSSET, J., BOULÊTREAU, S., VILLÉGER, S., STRECKER, A.L. & GRENOUILLET, G. (2016) Increased taxonomic and functional similarity does not increase the trophic similarity of communities. *Global Ecology and Biogeography* **25**, 46–54.

POST, D.M., LAYMAN, C.A., ARRINGTON, D.A., TAKIMOTO, G., QUATTROCHI, J. & MONTAÑA, C.G. (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**, 179–189.

R CORE TEAM (2013) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

ROSENBLATT, A.E. & SCHMITZ, O.J. (2016) Climate change, nutrition, and bottom-up and top-down food web processes. *Trends in Ecology & Evolution*.

SCHLUTER, D. (1995) Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology* **76**, 82–90.

SCHMIDT, S.N., HARVEY, C.J. & VANDER ZANDEN, M.J. (2011) Historical and contemporary trophic niche partitioning among Laurentian Great Lakes coregonines. *Ecological Applications* **21**, 888–896.

SHOUP, D.E. & WAHL, D.H. (2009) The effects of turbidity on prey selection by piscivorous largemouth bass. *Transactions of the American Fisheries Society* **138**, 1018–1027.

SIBBING, F.A. & NAGELKERKE, L.A.J. (2001) Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Reviews in Fish Biology and Fisheries*, 46.

SKULASON, S. & SMITH, T.B. (1995) Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution* **10**, 366–370.

SMITH, T.B. & SKULASON, S. (1996) Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics* **2**, 111–133.

SYMONDS, M.R.E. & MOUSSALLI, A. (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* **65**, 13–21.

TERBORGH, J. & ESTES, J.A. (2010) *Trophic cascades: predators, prey and the changing dynamics of nature.* Island Press, Washington DC.

TILMAN, D. (1982) *Resource competition and community structure.* Princeton University Press, Princeton, NJ.

VAN VALEN, L. (1965) Morphological variation and width of ecological niche. *The American Naturalist* **99**, 377–390.

VANNOTE, R.K., MINSHALL, G.W., CUMMINS, K.W., SEDELL, J.R. & CUSHING, C.E. (1980) The River continuum concept. *Canadian Journal of Zoology* **37**, 130–137.

VILLÉGER, S., BROSSE, S., MOUCHET, M., MOUILLOT, D. & VANNI, M.J. (2017) Functional ecology of fish: current approaches and future challenges. *Aquatic Sciences* **79**, 783-801.

VILLÉGER, S., MIRANDA, J.R., HERNÁNDEZ, D.F. & MOUILLOT, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* **20**, 1512–1522.

VIOLLE, C., NAVAS, M.-L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. & GARNIER, E. (2007) Let the concept of trait be functional! *Oikos* **116**, 882–892.

VREDE, T., DRAKARE, S., EKLÖV, P., HEIN, A., LIESS, A., OLSSON, J., PERSSON, J., QUEVEDO, M., STABO, H.R. & SVANBÄCK, R. (2011) Ecological stoichiometry of Eurasian perch - intraspecific variation due to size, habitat and diet. *Oikos* **120**, 886–896.

ZANDONÀ, E., DALTON, C.M., EL-SABAAWI, R.W., HOWARD, J.L., MARSHALL, M.C., KILHAM, S.S., REZNICK, D.N., TRAVIS, J., KOHLER, T.J., FLECKER, A.S., THOMAS, S.A. & PRINGLE, C.M. (2017) Population variation in the trophic niche of the Trinidadian guppy from different predation regimes. *Scientific Reports* **7**: 5770.

ZHAO, T., VILLÉGER, S., LEK, S. & CUCHEROUSSET, J. (2014) High intraspecific variability in the functional niche of a predator is associated with ontogenetic shift and individual specialization. *Ecology and Evolution*, 4649–4657.

Supplementary information for chapter V.

Table V. S1. Calculation of the ten functional traits and their ecological meanings (adapted from Villéger *et al.,* 2010 and Zhao *et al.*, 2014).

Functional traits	Calculation	Ecological meaning
Body mass	M	Mass, volume
Oral gape surface	$\frac{Mw * Md}{Bw * Bd}$	Size of resource items
Oral gape shape	$\frac{Md}{Mw}$	Shape of resource items
Oral gape position	$\frac{Mo}{Hd}$	Position of resource items in water column
Gut length	$\frac{Gl}{Bl}$	Capacity to digest vegetal material
Eye size	$\frac{Ed}{Hd}$	Capacity to detect preys
Eye position	$\frac{Eh}{Hd}$	Position of resource items in water column
Body transversal shape	$\frac{Bd}{Bw}$	Preferential position in the water column, hydrodynamism
Body transversal surface	$\frac{\ln\left(\left(\frac{\pi}{4}\times Bw \times Bd\right)+1\right)}{\ln\left(M+1\right)}$	Mass distribution along the body and hydrodynamism
Pectoral fin position	$\frac{PFi}{PFb}$	Manoeuvrability
Caudal peduncle throttling	$\frac{CFd}{CPd}$	Propulsion efficiency and swimming endurance

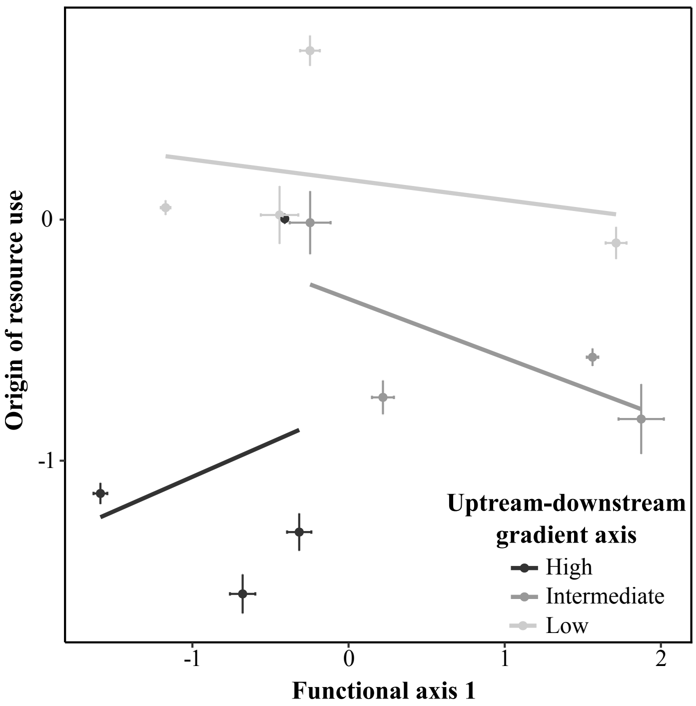


Figure V.S1. Relationship between the functional axis 1 and the origin of resource use is dependent on the upstream-downstream gradient axis (displayed as categorical for visualisation purpose). Error bars represent ± 1 SE.

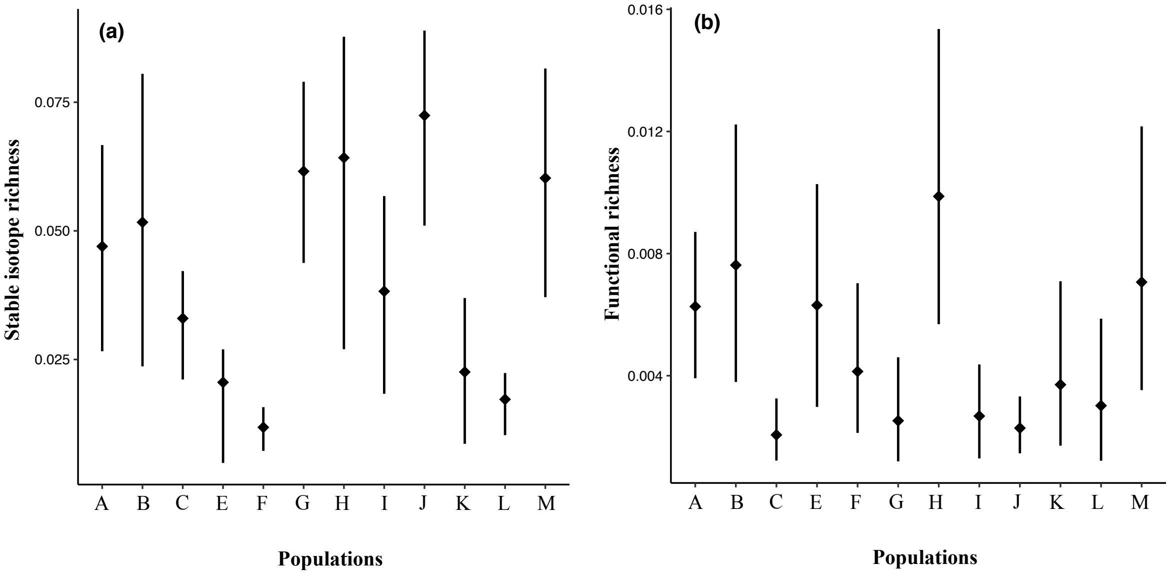


Figure V.S2. Stable isotope **(a)** and functional **(b)** richness in each population. Points represent median values and bars 95% percentile interval obtained from bootstrapping.

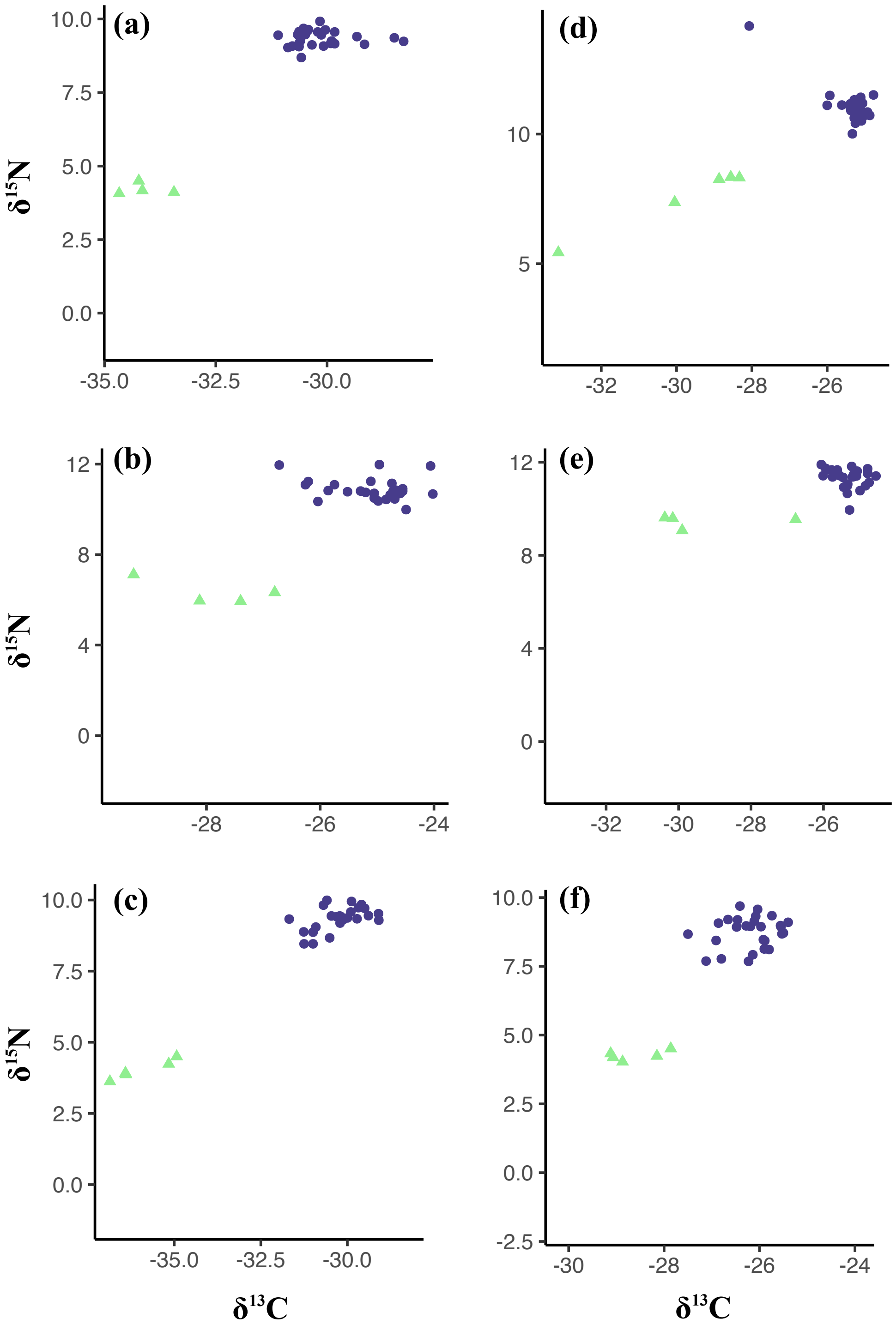


Figure V.S3. Raw δ^{15}N and δ^{13}C values (‰) from populations A to F in panels (a) to (f), respectively. Circles represent individual fish and triangle invertebrate samples.

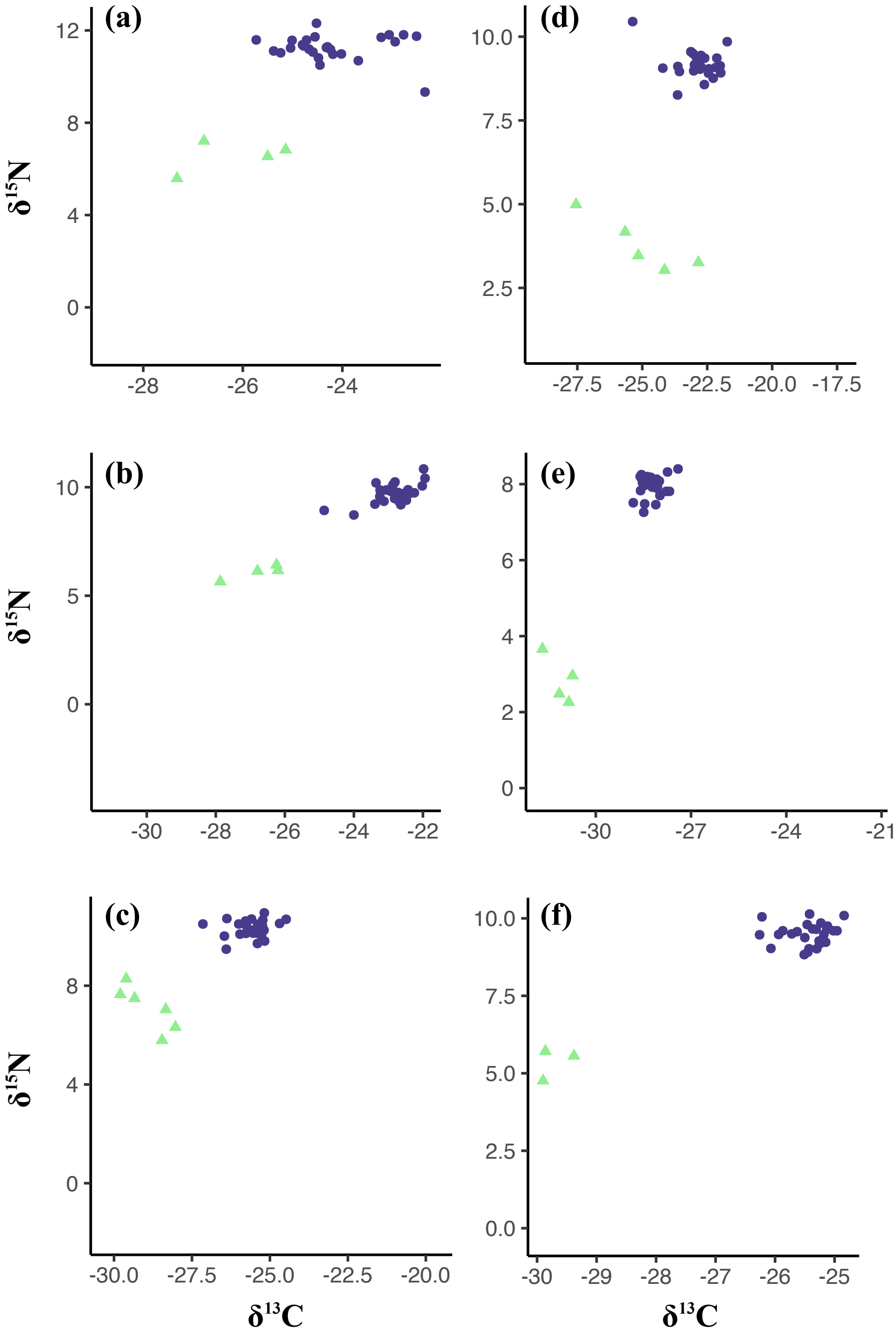


Figure V.S4. Raw δ^{15}N and δ^{13}C values (‰) from populations G to L in panels (a) to (f), respectively. Circles represent individual fish and triangle invertebrate samples.

Chapitre VI.

Intraspecific variation and warming have comparable effects on eco-evolutionary dynamics.

Allan Raffard[1,2], Julien Cucherousset[3], Frédéric Santoul[2], Lucie Di Gesu[1], & Simon Blanchet[1,3]

[1] CNRS, Université Toulouse III Paul Sabatier, Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UMR-5321, F-09200 Moulis, France.

[2] EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France.

[3] Laboratoire Évolution et Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, IRD, UPS, 118 route de Narbonne, Toulouse 31062, France.

Manuscript in preparation for submission in **Global Change Biology**.

Résumé

Les divergences évolutives entre populations d'une même espèce peuvent affecter le fonctionnement des écosystèmes, ce qui peut en retour affecter les trajectoires évolutives des populations. Ces boucles de rétroaction éco-évolutives ont récemment été démontrées. Cependant, leur importance écologique comparée à celle de facteurs écologiques clés est encore inconnue. Dans cette étude, nous avons montré expérimentalement que la variation intraspécifique chez le vairon commun (*Phoxinus phoxinus*) a eu des conséquences écologiques et trans-générationnelles aussi fortes qu'une augmentation de 2°C de la température. Plus précisément, la variation de deux traits phénotypiques (masse corporelle et taux de croissance) entre des vairons adultes a eu des effets sur la structure des communautés et le fonctionnement des écosystèmes, ce qui a entrainé des effets sur la survie et la croissance de juvéniles de vairons. Ces conséquences éco-évolutives étaient indépendantes de celles induites par la température. Nous avons conclu que la variation intraspécifique était un facteur écologique majeur, suggérant que les boucles de rétroactions éco-évolutives devraient être prises en compte pour quantifier les conséquences des changements globaux.

Abstract

Evolutionary divergences occurring within species can affect the way organisms shape their environment, which can in turn affect their own evolutionary trajectories. These eco-evolutionary feedbacks have recently been demonstrated, but their relevance compared to that of key environmental drivers in the dynamics of biological systems is still unknown. Here, we experimentally showed that intraspecific variation in the European minnow (*Phoxinus phoxinus*) led to ecological and transgenerational effects that are as strong as those of warming ecosystems by 2°C. Specifically, variations in two phenotypic traits (body size and growth rate) in adult minnows led to environmental changes that subsequently modulated fitness traits of juvenile minnows. Importantly, the eco-evolutionary consequences of intraspecific variation were different and independent from those induced by warming. We conclude that intraspecific variation is an indisputable driver of ecological and evolutionary dynamics, which suggests that eco-evolutionary feedbacks should not be neglected when quantifying the consequences of global change.

Introduction

Reciprocal interactions between ecological and evolutionary dynamics occurring over contemporary time scales (*eco-evolutionary dynamics*) have been increasingly studied in the last two decades (Thompson, 1998; Schoener, 2011; Hendry, 2016). Theory predicts that evolutionary diversification within a species can affect ecological processes such as primary productivity, resulting in environmental changes that can act as new selective pressures modulating the fitness and the evolution of organisms (Odling-Smee *et al.*, 2013; Hendry, 2016). These reciprocal interactions can generate eco-evolutionary feedbacks linking species evolution and ecosystem functioning, providing an integrative and temporally dynamic framework for understanding biological systems (Matthews *et al.*, 2011). Although the study of eco-evolutionary feedback loops has long been conceptual (Thompson, 1998; Matthews *et al.*, 2011), recent experimental studies have demonstrated the existence of these processes (Turcotte, Reznick, & Daniel Hare, 2013; Matthews *et al.*, 2016; Brunner *et al.*, 2017; Best *et al.*, 2017). However, the relative importance of eco-evolutionary feedbacks in the dynamics of natural ecosystems has been questioned (Thompson, 1998; Schoener, 2011).

To answer this question, it is important to determine whether intraspecific variation is negligible (or not) compared to key environmental drivers affecting both ecological and evolutionary dynamics, such as temperature, nutrient availability, predation or parasitism (Schoener, 2011; Rudman *et al.*, 2018). Recent investigations have revealed that intraspecific variation (emerging from evolutionary diversification) can affect ecological processes with an intensity similar to that of key environmental drivers (El-Sabaawi *et al.*, 2015; Des Roches *et al.*, 2018). However, whether the ecological effects mediated by intraspecific variation are strong and persistent enough to affect fitness traits of subsequent generations, and whether these transgenerational effects are similar to those of indisputably important environmental drivers is still unknown. Addressing this question is an important first step to determining the relative contribution of eco-evolutionary feedbacks in driving the responses of biological systems to varying environmental conditions (Rudman *et al.*, 2018).

Here, we experimentally quantified the consequences of intraspecific variation on ecological processes and subsequent evolutionary trajectories, and then compared these consequences to the ecological and evolutionary consequences of warming. Temperature is a key abiotic factor that strongly varies at the landscape scale, directly affects key ecological functions such as primary productivity and ecosystem respiration (Yvon-Durocher *et al.*, 2010, 2015), and imposes a strong selective pressure on organism traits (Brown *et al.*, 2004;

Parmesan, 2006; Rey *et al.*, 2016). Recent changes in climate worldwide have also raised major concerns regarding the ecological and evolutionary consequences of this major facet of global change (Parmesan, 2006; Yvon-Durocher *et al.*, 2010). Comparing the eco-evolutionary consequences of intraspecific variation to those of changes in temperature hence provides a strong test for unraveling whether modifying patterns of intraspecific variation is trivial or not for biological dynamics. We ran a two-phase "common gardening experiment" (*sensu* Matthews *et al.*, 2011, 2016, Figure VI.1) and manipulated (i) intraspecific variation in a freshwater fish (European minnow, *Phoxinus phoxinus*) by selecting individuals from six distinct populations (i.e., differences in genotypes and functional traits, Figures VI.S1 and VI.S2) and (ii) water temperature by setting mesocosms to differ by 2°C throughout the experiment (Figure VI.S3). An increase in temperature of 2°C represents the general warming expectations for freshwaters over the next 40 years (IPCC, 2014). During the first experimental phase (*ecological effects*, 10-weeks), we compared the strengths of the effects of intraspecific variation among adult minnows, to the strengths of the effects of warming on prey community structure and ecosystem functions (Figure VI.1). Adults were then removed from the mesocosms and replaced by juveniles with a common origin for the second experimental phase (*transgenerational effects*, 11-weeks). We tested how the ecological variations induced during the first phase (due to intraspecific variation and/or warming) affected the evolutionary trajectories (fitness and performance) of juveniles.

Material and Methods

Study species

European minnow (*Phoxinus phoxinus*) was used as the model species. *P. phoxinus* is a small-bodied (maximum length: ~80 mm, mean generation time: ~2 years) cyprinid fish species widely distributed in Western Europe. *P. phoxinus* lives in relatively cold waters, mainly in streams and rivers but also in mountain lakes (Keith *et al.*, 2011). It is a generalist species that feeds on small invertebrates, algae, zooplankton and small fish larvae (Keith *et al.*, 2011).

In September 2016, we collected adult minnows by electrofishing in six rivers in southwestern France (Figure VI.S1). We selected populations that were isolated geographically (minimal riparian distance among sites = 64 km, mean ± SD = 343 km ± 182) and had distinct environments (Figure VI.S4) to favor both genetic and phenotypic divergences among populations. Accordingly, the mean genetic divergence among populations was F_{st} = 0.162 (measured using 17 microsatellites, min-max = 0.043-0.313), indicating a high evolutionary distinctiveness among the populations. The body mass (a highly heritable, Carlson & Seamons, 2008, and important functional trait, Woodward *et al.*, 2005, Figure VI.S2) of the sampled populations also varied, as did two other important functional traits (Brown *et al.*, 2004; McIntyre *et al.*, 2008): the metabolic (min-max = 0.1388-0.2737 mg $O^{2}.g^{-1}.h^{-1}$, F = 14.599, d.f = 5,188, $p < 0.001$) and ammonium excretion (min-max = 17.02-43.48 µg $NH^{4+}.g^{-1}.L^{-1}.h^{-1}$, F = 4.695, d.f = 5,175, $p < 0.001$, Chapter IV) rates. All fish collections and husbandry for adults and juveniles were conducted in accordance with sampling permits obtained from local authorities (25-08-2016, 24-05-2016, 09-273, SA-013-PB-092, A09-3). Fish from different populations were reared at a similar density and separately for ~6 months in 1100 L outdoor tanks to minimize previous environmental effects on phenotypes. During rearing, the fish were fed ad-libitum with a mixture of pelletized food and dead chironomids until the start of the experiment.

Phase 1: effects of intraspecific variation and temperature on ecological processes

The experiment consisted of 72 replicated mesocosms placed in a greenhouse with a 12:12 h light-dark photoperiod. Mesocosms were filled with 100 L of tap water and 1 cm of gravel covering the bottom of each tank. Tanks were covered with a 1 cm plastic mesh net to prevent fish escapes. Nutrients were added to the mesocosms using 5 mL of solution containing nitrogen and phosphorus (ratio N: P: K = 3.3: 1.1: 5.8) on December 2nd 2016. Each mesocosm was then inoculated with 200 mL of a concentrated solution of phytoplankton from a unique lake origin (Lake Lamartine, France 43°30'21.5"N, 1°20'32.7"E) on December 12th 2016. Two months later (February 15th 2017), an additional 200 mL of concentrated solution of zooplankton from the same lake was added to each mesocosm. Finally, we inoculated each mesocosm with sediment and macroinvertebrates (i.e., mainly Gastropoda and Bivalvia) from Lake Lamartine.

Each tank was assigned to one of twelve treatments according to a full-factorial design with intraspecific variation (i.e., population origin, six levels corresponding to each population) and temperature (two levels: low and high temperature) as the main factors (Figure VI.1). Each treatment was replicated six times. Water temperature was controlled and adjusted using a *Blue Marine*® water chiller and a stainless steel coil placed in each tank through which a flux of water (independent from the water of the tanks) flowed at either 18°C or 21°C. Natural seasonal temperature variations occurred; on average, the low and high water temperature treatments differed by 2.08°C according to seasonal variations (Figure VI.S3).

In March 2017, adult fish were weighed to the nearest 0.01 g and a single fish was introduced to each mesocosm. This individual-based approach prevented the experimental ecosystems from collapsing due to the over-density of top consumers and allowed the ecological effects of individual phenotypes to be measured. After 73 days (Figure 1), each fish was removed, weighed and euthanized in a solution of benzocaine at 25 mg.L^{-1}. The growth rate (%.day^{-1}) of the adults was calculated as the specific growth rate (SGR): $SGR = \frac{ln(Wf)-ln(Wi)}{T} * 100$, where Wf and Wi are the final and initial body masses, respectively, and T is time interval between two measurements (in days). Concomitantly, we measured multiple community and ecosystem parameters to evaluate differences in ecological processes among treatments.

(*i*) Pelagic algae stock was assessed as a proxy of pelagic primary productivity. Measurements were performed using a portable spectrometer (AlgaeTorch, bbe Moldaenke®) to assess the chlorophyll-a concentration (µg/L) in the water column. Two measurements were taken in each mesocosm and were averaged for the analyses.

(*ii*) Benthic algae stock was assessed as a proxy of the benthic primary productivity using a portable spectrometer (BenthoTorch, bbe Moldaenke®). The chlorophyll-a concentration (µg/cm^2) was measured on two tiles (20 x 20 cm) placed in the mesocosms the day before the start of the experiment. These measurements were averaged for analyses.

(*iii*) The abundance of filamentous algae was quantified. Filamentous algae cover (%) was visually estimated by two operators, and values were averaged for analyses.

(*iv*) Zooplankton community was assessed by filtering 5 L of water through a 200 µm sieve. Samples was conserved in a 70% ethanol solution and subsequently identified to the order or family levels, including Copepoda (i.e., Cyclopoida and Calanoida) and Cladocera (i.e., Daphniidae, Chydoridae and Bosminidae). Zooplankton size was assessed by measuring 10 individuals of each order and family level from each mesocosm to the nearest 0.001 mm using ImageJ®.

(*v*) Decomposition rate was measured by quantifying the mass loss of black poplar (*Populus nigra*, a dominant riparian tree in southern France) abscised leaves (Alp *et al.*, 2016). One day before the start of the experiment, 4 g of air-dried leaves were put in each mesocosm within a coarse mesh (1 x 1 cm) bag. At the end of the phase 1, the remaining leaf material was removed from the mesocosms, rinsed with tap water, oven dried at 60°C for three days and weighed to the nearest 0.001 g to assess the loss of biomass. The decomposition rate was calculated as $k = -\frac{ln\,(X)}{t}$ (Alp *et al.*, 2016), where X is the proportion of litter remaining after phase 1 and t is the elapsed time in days.

(*vi*) Macroinvertebrates (> 1 mm, essentially molluscs) were collected from the mesh bags used to measure decomposition rates, conserved in a 70% ethanol solution, and identified as Bivalvia or Gastropoda.

(*vii*) Abiotic parameters of the water [pH, specific conductance (µS), oxygen concentration (mg.L^{-1}) and turbidity (NTU)] were measured with a multiparameters probe (YSI Pro DSS Water Quality Meter®). We summarized these parameters using principal component axis (PCA) (package ade4 in R, Chessel, Dufour, & Dray, 2007). We selected the first axis of the PCA as the synthetic variable. This axis explained 60% of the variance and was correlated to the oxygen concentration (loading component: -0.95), pH (-0.93), specific conductance (0.70) and, to a lesser extent, turbidity (0.25).

Phase 2: effects of ecological differences on juvenile fitness

After the removal of adult fish on June 13th 2017, 45 juvenile minnows were introduced to each mesocosm. We used juveniles from a single origin (i.e., fish farm, *Amorvif EURL*) to control for potential genetic effects. Juveniles were introduced as soon as possible after hatching to increase the possibility of differential mortality and/or ontogenetic plasticity. Therefore, juveniles were introduced when they were only two weeks old as stage III larvae (Pinder, 2001) (Figure VI.S5). They were not manipulated (i.e., weighted and/or measured) before being randomly introduced in the mesocosms to limit potential mortality. The juveniles were removed from the mesocosms 79 days later, and we measured several proxies for their fitness. Individuals were counted to assess survival, weighed to the nearest 0.001 g to assess growth rate (assuming all juveniles had the same initial body mass, we used the final body mass of juveniles as a measure of growth rate), and measured in length to the nearest 0.1 mm (using ImageJ) to assess the body condition, which was calculated as the residuals of the relationship between individual body mass and length.

Statistical analyses

Two adult individuals died before the end of phase 1, so we discarded these two replicates from the analyses. Moreover, we identified six tanks in which crayfish had been inadvertently introduced; we discarded these six replicates because crayfish are known to have disproportionally strong impacts on ecosystems (Alp *et al.*, 2016). As such, the final analyses were run on 64 replicates.

First, we compared the magnitude of the effects of intraspecific variation and temperature on ecological (phase 1) and evolutionary (phase 2) dynamics. To do so, we used a meta-analytic approach consisting of first running linear models linking each ecological or evolutionary parameter (dependent variables) to the explicative variables, i.e., intraspecific variation (categorical factor, six levels), temperature (categorical factor, two levels) and the resulting two-term interaction. The interaction term was removed when nonsignificant because it prevents the interpretation of simple terms (Nakagawa & Cuthill, 2007). From these linear models, we calculated the standardized effect sizes eta squared (Levine & Hullett, 2002) (η^2) as follows: $\eta^2 = SS_x/SS_{tot}$, where SS_x is the sum of squares for the effect of interest (intraspecific variation, temperature or the interaction term, if significant) and SS_{tot} is the total sum of squares. Sums of squares were extracted from type II analysis of variance when the interaction was not in the model and from type III analysis of variance when the interaction was significant (Langsrud, 2003). Finally, the mean effect size (MES) values of intraspecific variation and temperature across the ecological or evolutionary parameters were compared using t-test.

Next, we assessed the direct and indirect links between intraspecific variation, temperature, and the ecological and evolutionary parameters using a causal analysis. Since we aimed at identifying the mechanisms by which the mesocosms diverged, we included the initial body mass and the growth rate of adult fish from phase 1 because these two traits are known to drive ecological processes (Woodward *et al.*, 2005). We used path analyses (Grace, 2006; Grace *et al.*, 2016; Duffy *et al.*, 2016) to set a full model based on biologically rational paths and the visual inspection of the variance-covariance matrix, and all variables were scaled to the mean to facilitate the comparison. This full model was then simplified by removing sequentially weak and/or nonsignificant paths until reaching a model that was correct statistically (i.e., a model that best fit the observed covariance matrix based on the maximum likelihood χ^2 statistic, Grace, 2006), while leading to the lowest Akaike Information Criteria (AIC) value. We finally extracted the absolute values of path coefficients from the final model to tease apart the direct and indirect effects of body mass, growth rate and temperature on the ecological and evolutionary parameters. Statistical analyses were performed using R software (R Core Team, 2013), and path analyses were run using Amos (Arbuckle, 2014).

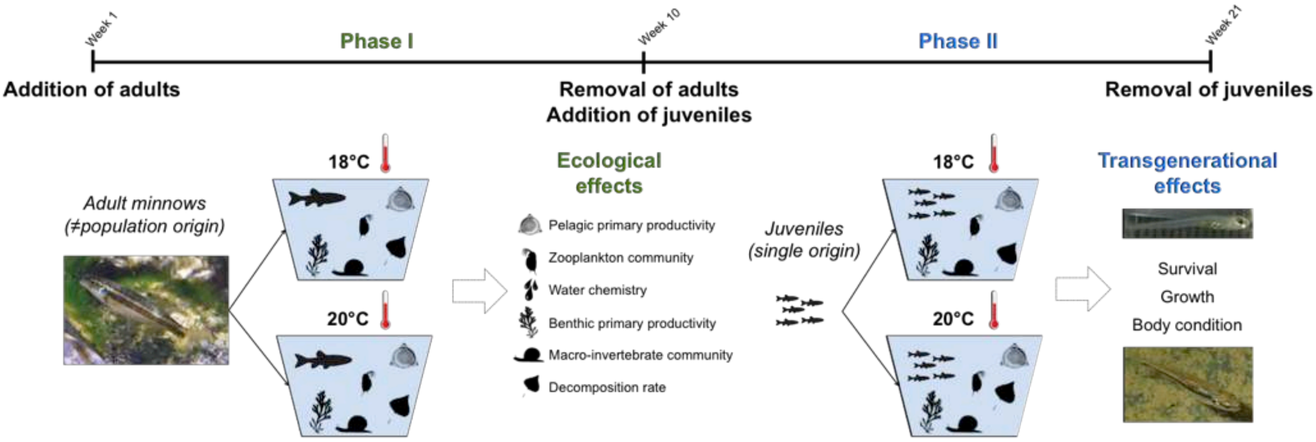


Figure VI.1. Experimental design used to test the ecological (phase 1) and transgenerational (phase 2) effects of intraspecific variation among adult minnows (*Phoxinus phoxinus*) and warming.

Results

In the first phase, we found that the effects of intraspecific variation in adult minnows on ecological processes (measured over all ecological parameters) were at least as strong as those of warming on ecological processes (mean effect size (MES) ± standard error = 0.103 ± 0.018 and MES ± SE = 0.078 ± 0.036 for intraspecific variation and warming, respectively; $t = 0.624$, d.f = 18, $p = 0.540$, Figure VI.2). Nonetheless, the effects were heterogeneous across ecological parameters (Figure VI.2b, Figure VI.S6). For instance, intraspecific variation had the strongest ecological effect on the abundance of Cladocera, whereas warming had a particularly strong ecological effect on decomposition rate (Figure VI.2b, Figure VI.S7 and VI.S8). A single interaction term between warming and intraspecific variation was significant (i.e., for benthic primary productivity, $F = 10.831$, d.f = 5,52, $p = 0.022$), indicating that the ecological effects of intraspecific variation were not temperature-dependent for most ecological parameters. The body mass and growth rate of minnows, two functionally important traits differing among minnow populations (although the later was also affected by experimental temperature, Figure VI.S2), were included in a path analysis testing the direct and indirect relationships among trait variation, warming and ecological parameters. We found that intraspecific variation in these two functional traits affected ecological processes as much as warming and that body mass was the most influential functional trait (Figure VI.3). We further found that the intraspecific trait variation acted both directly and indirectly on ecological parameters (Figure VI.3b). For instance, adult body mass affected the abundance of Copepoda directly, subsequently leading to an indirect effect on the abundance of Cladocera (Table VI.1, Figure VI.3a). The ecological effects of warming were mainly direct (67%), although some indirect effects were also observed (Figure VI.3b). For instance, warming directly increased Bivalvia abundance, positively affecting the abundance of Copepoda and the size of Cladocera, hence representing an indirect effect of warming on the zooplankton community (Figure VI.3).

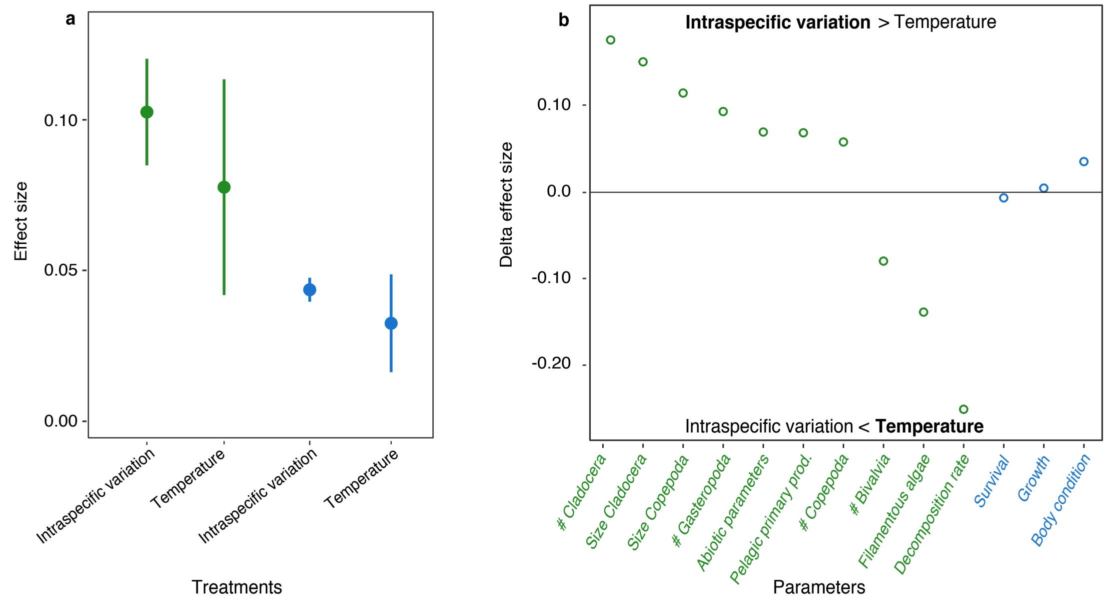


Figure VI.2. Comparison of the ecological and transgenerational effects of intraspecific variation and warming. **(a)** Eta squared (η^2) effect size of the intraspecific variation among adults and temperature on ecological (green) and fitness (blue) parameters. Error bars represent ± 1 SE. **(b)** Delta of effect sizes (η^2) of intraspecific variation and temperature on ecological and fitness parameters. Positive values indicate a higher effect of intraspecific variation, and negative values indicate a higher effect of temperature.

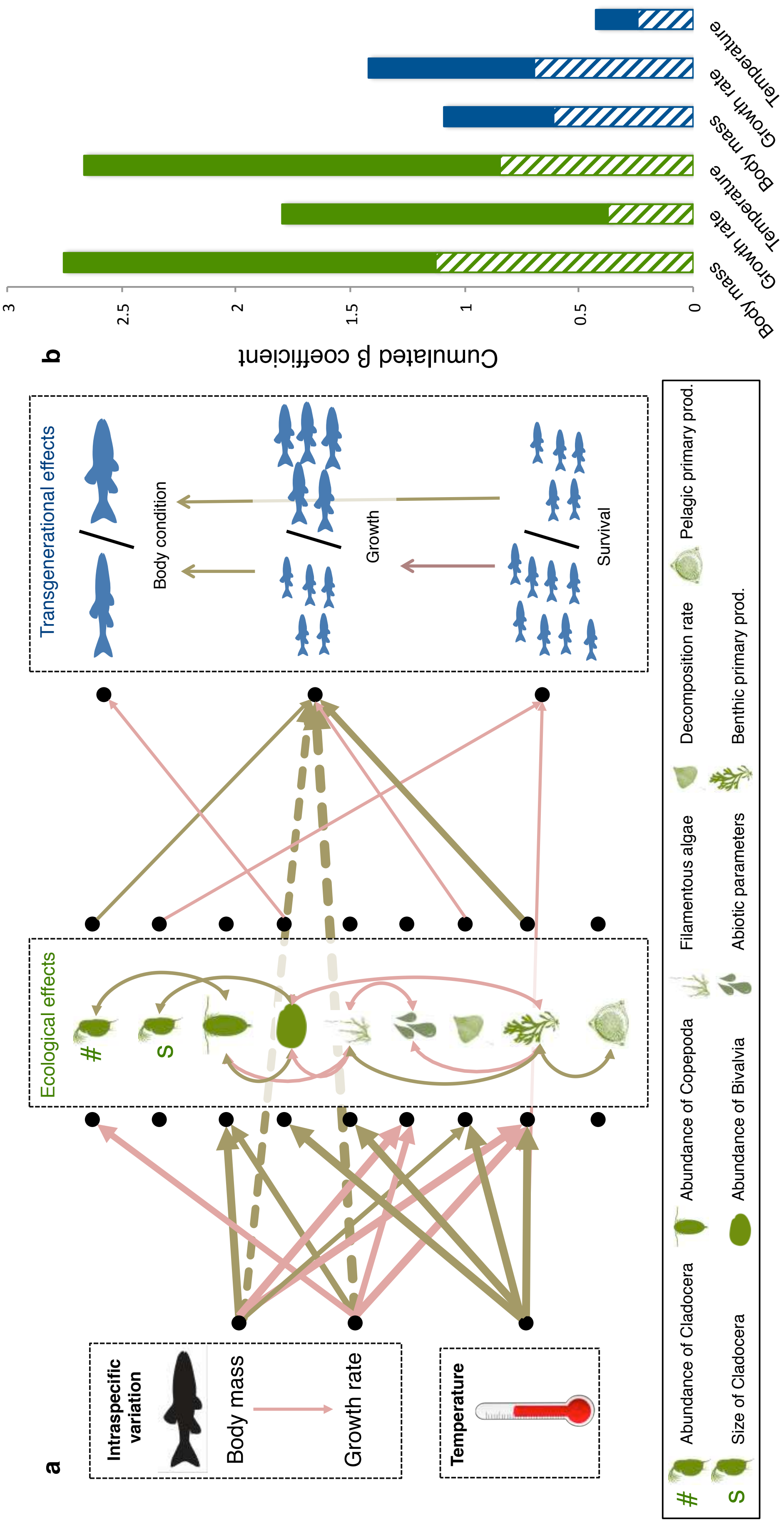
Table VI.1. Causal pathways between variations in intraspecific traits (body mass$_{\text{adults}}$ and growth rate$_{\text{adults}}$), temperature and ecological parameters and fitness traits obtained from path analyses.

Response	Effect	Path coefficient	S.E.	*p*-value
Growth rate$_{\text{adults}}$	Body mass$_{\text{adults}}$	-0.674	0.093	< 0.001
Cladocera abundance	Growth rate$_{\text{adults}}$	-0.341	0.111	0.002
	Copepod abundance	0.339	0.11	0.002
Size Cladocera	Bivalve abundance	0.428	0.114	< 0.001
Copepoda abundance	Growth rate$_{\text{adults}}$	0.37	0.153	0.016
	Bivalve abundance	0.311	0.113	0.006
	Body mass$_{\text{adults}}$	0.477	0.153	0.002
Bivalvia abundance	Temperature	0.441	0.113	< 0.001
Abiotic parameters	Body mass$_{\text{adults}}$	-0.289	0.124	0.019
	Filamentous algae	-0.644	0.092	< 0.001
	Growth rate$_{\text{adults}}$	-0.194	0.124	0.116
Pelagic prod.	Prod. benthic	0.244	0.12	0.043
Benthic prod.	Growth rate$_{\text{adults}}$	-0.522	0.139	< 0.001
	Bivalvia abundance	-0.228	0.118	0.054
	Body mass$_{\text{adults}}$	-0.486	0.139	< 0.001
	Temperature	0.292	0.132	< 0.001
	Filamentous algae	0.239	0.12	0.047
Decomposition rate	Body mass$_{\text{adults}}$	0.375	0.132	< 0.001
	Temperature	0.532	0.096	< 0.001
Filamentous algae	Temperature	0.554	0.118	< 0.001
	Bivalvia abundance	-0.207	0.123	0.092
	Copepoda abundance	-0.168	0.110	0.126
Survival$_{\text{juveniles}}$	Size Cladocera	-0.195	0.123	0.112
	Temperature	-0.183	0.123	0.135

Table VI.1. (continued)

Growth rate$_{\text{juveniles}}$	Body mass$_{\text{adults}}$	0.479	0.130	< 0.001
	Growth rate$_{\text{adults}}$	0.725	0.125	< 0.001
	Prod. benthic	0.332	0.092	< 0.001
	Cladocera abundance	0.250	0.089	0.005
	Survival$_{\text{juveniles}}$	-0.566	0.084	< 0.001
	Decomposition rate	-0.234	0.093	0.012
Body condition$_{\text{juveniles}}$	Bivalve abundance	-0.175	0.073	0.016
	Survival$_{\text{juveniles}}$	0.556	0.087	< 0.001
	Growth rate$_{\text{juveniles}}$	0.941	0.083	< 0.001

In the second phase (Figure VI.1), we found that the strength of the effect sizes of intraspecific variation and warming on the fitness proxies (survival, growth rate and body condition) were similar (MES ± SE = 0.044 ± 0.004 and MES ± SE = 0.032 ± 0.016 for intraspecific variation and warming, respectively, $t = 0.665$, d.f = 4, $p = 0.542$, Figure VI.2). Notably, the average effect sizes of intraspecific variation and warming on the fitness proxies were half the intensity of those on ecological parameters (Figure VI.2), indicating that transgenerational effects induced by the initial treatments were weakest in average than ecological effects observed in the first phase. Nonetheless, we found evidence for eco-evolutionary feedbacks since the juvenile growth rate was related to the ecological parameters (benthic primary productivity, decomposition rate and Cladocera abundance), which were controlled by intraspecific variation (Figure VI.3a). Juvenile survival was also related to juvenile growth rate (density-dependent growth rate) and was indirectly related to warming. We also identified a direct relationship between adult trait variation and juvenile growth rate (Figure VI.3), which was unexpected given that the adults were removed from the tanks before the juveniles were introduced. This result indicates intraspecific variation had unmeasured indirect effects (mediated by ecological changes) on fitness proxies of the subsequent generation. Juvenile survival was negatively related to the body size of Cladocera and negatively related to temperature (i.e., survival increased as temperature decreased). Juvenile body condition covaried with both juvenile survival and growth rate and was lower when the abundance of Bivalvia, which was directly affected by temperature, was high (Figure VI.3).


a
Intraspecific variation
Body mass
Growth rate
Temperature
Ecological effects
#
S
Transgenerational effects
Body condition
Growth
Survival
Abundance of Cladocera
S Size of Cladocera
Abundance of Copepoda
Abundance of Bivalvia
Filamentous algae
Abiotic parameters
Decomposition rate
Benthic primary prod.
Pelagic primary prod.
b
Cumulated β coefficient
0
0.5
1
1.5
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2.5
3
Body mass
Growth rate
Temperature
Body mass
Growth rate
Temperature

Figure VI.3. Ecological and transgenerational effects of intraspecific trait variation and warming. **(a)** Representation of the simplified path analysis linking intraspecific trait variation among adult minnows, temperature, and their ecological and transgenerational effects. The covariance structure of this simplified path model, which contains both ecological and fitness parameters, did not differ from that of the data ($\chi^2 = 65.373$, d.f = 72, $p = 0.696$), indicating that the data were well supported by the model. The arrow line width is proportional to the β path coefficients (brown and pink arrows represent positive and negative values, respectively), and the dotted lines represent indirect effects of intraspecific variation on fitness parameters. **(b)** Cumulated absolute β path coefficients extracted from the simplified path analysis depicting the direct (filled) and indirect (hatched) relationships between intraspecific trait variation among adult minnows, temperature, ecological dynamics (green) and evolutionary dynamics (blue). Note that the direct effects of intraspecific variation on fitness parameters are not true direct effects (because the adult fish were removed before phase 2 of the experiment) but instead reveal unmeasured causal relationships. # = *abundance.*

Discussion

We found that the ecological consequences of intraspecific variation and warming were similar in strength but acted on different ecological processes. Adult minnows from distinct populations modulated both the abundance and the size of their prey (zooplankton Cladocera), probably because these populations have different prey consumption and selectivity characters. In contrast, warming strongly accelerated leaf litter decomposition, probably because warmer temperatures stimulate bacterial activity (Brown *et al.*, 2004; Yvon-Durocher *et al.*, 2015). The transgenerational effects of intraspecific variation and warming were also similar in strength, regardless of the fitness traits investigated. For instance, the survival of juvenile minnows was higher in the low-temperature than in the high-temperature treatment (which is expected given that minnows inhabit relatively cold rivers, Keith *et al.*, 2011), whereas the growth rate of juveniles differed depending on the adult minnow population introduced at the onset of the experiment. Notably, the effects of warming on the evolutionary trajectories of juveniles might be overestimated compared to the effects of intraspecific variation, since the former represents the cumulative results of both second-phase direct effects and first-phase indirect effects mediated by ecological changes. Overall, our results demonstrate that intraspecific variation can affect the ecological and evolutionary dynamics of biological systems as much as warming does, although in different directions.

In this study, we used wild-caught individuals to reflect the actual ecological and evolutionary effects intraspecific variation may have. A drawback of this approach is that the plastic (environmental) and genetic contributions (due to drift and/or selection) of intraspecific variation to ecological and evolutionary dynamics cannot be properly teased apart. Nonetheless, there was a high genetic differentiation among targeted populations (F_{st} = 0.162, see methods), traits used to quantify the effects of intraspecific variation (i.e., body mass and growth rate) are highly heritable and are affected by natural selection in many ectotherms (including fish species, Carlson & Seamons, 2008), and minnows were raised a quarter of generation in a common environment to buffer -to some extent- the plastic contribution. For these reasons, we can reasonably assume an evolutionary basis (either due to drift and/or selection) of intraspecific variation among the targeted minnow populations, which suggests that eco-evolutionary feedbacks likely occur in this biological system, and significantly modulate the whole biological dynamics of ecosystems. This eco-evolutionary feedback comprised indirect effects of intraspecific variation among adult minnows on the evolutionary trajectory of juveniles, which were mediated by the direct consequences of adult minnows on the ecological theatre. Currently, very few studies have demonstrated the existence of eco-evolutionary feedback, and most of have focused on model organisms (Turcotte *et al.*, 2013; Matthews *et al.*, 2016; Brunner *et al.*, 2017; Best *et al.*, 2017). Although this has to be taken with care since much remain to do to properly test for eco-evolutionary feedbacks in this model, our study extends the taxonomic scope of eco-evolutionary feedback loops and suggests that this process does not concern only species with strong eco-evolutionary divergences (Matthews *et al.*, 2011). We further identified two heritable traits (body mass and growth rate, Carlson & Seamons, 2008) that partially initiate these eco-evolutionary feedbacks and vary between adult minnows originating from environmentally and evolutionary distinct populations. Previous studies have identified growth rate and body mass as important traits for ecological processes (Woodward *et al.*, 2005), and we here provide novel insights into the indirect transgenerational consequences of these traits.

Interestingly, intraspecific variation and warming acted additively but not interactively on ecological and evolutionary dynamics. Indeed, we identified only one significant interaction between intraspecific variation and warming on benthic primary productivity, indicating that the effect of intraspecific variation on benthic primary productivity dynamics was temperature-dependent. This finding confirms that the ecological consequences of intraspecific variation are often independent from the abiotic context (El-Sabaawi *et al.*, 2015), which might also be the case for eco-evolutionary feedbacks. This independence is surprising, since local adaptation for specific fitness traits and/or for reaction norms often leads to strong context dependency in the responses of organisms to local abiotic conditions

(Kawecki & Ebert, 2004), and we may have observed cascading interactive effects of intraspecific variation on ecological and evolutionary dynamics (Rosenblatt & Schmitz, 2016). This finding is important because the absence of strong interactive effects reduces biological complexities and may therefore improve our ability to forecast the ecological and evolutionary consequences of environmental and biodiversity changes (Beckage, Gross, & Kauffman, 2011).

In conclusion, we demonstrated that the magnitude of the ecological and transgenerational effects of intraspecific variation was as strong as the effects of warming. This finding, combined to previous studies having compared the effects of intraspecific variation to that of biotic factors (e.g., density, Matthews *et al.*, 2016; Brunner *et al.*, 2017; Best *et al.*, 2017), strongly support the growing view that intraspecific variation and resulting eco-evolutionary feedbacks are not biologically negligible and should not be considered noise in ecosystems. Current environmental changes are rapid and can directly affect ecosystem functioning (Yvon-Durocher *et al.*, 2015). These changes can also directly modulate the distribution of intraspecific variation in landscapes and thereby indirectly affect the eco-evolutionary dynamics of biological systems (Matthews *et al.*, 2016; Brunner *et al.*, 2017). Our results reinforce recent reports that changes in intraspecific variations of wild populations (e.g., harvest, Palkovacs *et al.*, 2018, or pollution, Brodin *et al.*, 2013) could be as harmful as considerable environmental changes (e.g., warming) to biological dynamics and that this facet of biodiversity should therefore be conserved adequately (Mimura *et al.*, 2016).

Acknowledgements

We warmly thank Jose M. Montoya, Delphine Legrand and Jérôme G. Prunier for their valuable comments on a previous version of the manuscript. We thank Lucas Mignien, Kéoni Saint-Pe and Yoann Buoro for their help during the experimental work. AR was financially supported by a doctoral scholarship from the Université Fédérale de Toulouse. This work was undertaken at SETE and EDB, which is part of the “Laboratoire d’Excellence” (LABEX) entitled TULIP (ANR-10-LABX-41).

References

ALP, M., CUCHEROUSSET, J., BUORO, M. & LECERF, A. (2016) Phenological response of a key ecosystem function to biological invasion. *Ecology Letters* **19**, 519–527.

ARBUCKLE, J.L. (2014) Amos (Version 23.0) [Computer Program]. Chicago: IBM SPSS.

BECKAGE, B., GROSS, L.J. & KAUFFMAN, S. (2011) The limits to prediction in ecological systems. *Ecosphere* **2**, art125.

BEST, R.J., ANAYA-ROJAS, J.M., LEAL, M.C., SCHMID, D.W., SEEHAUSEN, O. & MATTHEWS, B. (2017) Transgenerational selection driven by divergent ecological impacts of hybridizing lineages. *Nature Ecology & Evolution* **1**, 1757–1765.

BRODIN, T., FICK, J., JONSSON, M. & KLAMINDER, J. (2013) Dilute concentrations of a psychiatric drug alter behavior of fish from natural populations. *Science* **339**, 814–815.

BROWN, J.H., GILLOOLY, J.F., ALLEN, A.P., SAVAGE, V.M. & WEST, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

BRUNNER, F.S., ANAYA-ROJAS, J.M., MATTHEWS, B. & EIZAGUIRRE, C. (2017) Experimental evidence that parasites drive eco-evolutionary feedbacks. *Proceedings of the National Academy of Sciences* **114**, 3678–3683.

CARLSON, S.M. & SEAMONS, T.R. (2008) A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. *Evolutionary Applications* **1**, 222–238.

CHESSEL, D., DUFOUR, A.B. & DRAY, S. (2007) ade4: Analysis of ecological data: exploratory and euclidean methods in multivariate data analysis and graphical display. R package version, 1–4.

DES ROCHES, S., POST, D.M., TURLEY, N.E., BAILEY, J.K., HENDRY, A.P., KINNISON, M.T., SCHWEITZER, J.A. & PALKOVACS, E.P. (2018) The ecological importance of intraspecific variation. *Nature Ecology & Evolution* **2**, 57–64.

DUFFY, J.E., LEFCHECK, J.S., STUART-SMITH, R.D., NAVARRETE, S.A. & EDGAR, G.J. (2016) Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences* **113**, 6230–6235.

EL-SABAAWI, R.W., BASSAR, R.D., RAKOWSKI, C., MARSHALL, M.C., BRYAN, B.L., THOMAS, S.N., PRINGLE, C., REZNICK, D.N. & FLECKER, A.S. (2015) Intraspecific phenotypic differences in fish affect ecosystem processes as much as bottom-up factors. *Oikos* **124**, 1181–1191.

GRACE, J.B. (2006) *Structural equation modeling and natural systems.* Cambridge University Press. Cambridge, UK.

GRACE, J.B., ANDERSON, T.M., SEABLOOM, E.W., BORER, E.T., ADLER, P.B., HARPOLE, W.S., HAUTIER, Y., HILLEBRAND, H., LIND, E.M., PÄRTEL, M., BAKKER, J.D., BUCKLEY, Y.M., CRAWLEY, M.J., DAMSCHEN, E.I., DAVIES, K.F., ET AL. (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* **529**, 390–393.

HENDRY, A.P. (2016) *Eco-evolutionary dynamics.* Princeton University Press.

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Core Writing Team, Pachauri, R.K., Meyer, L.A.). IPCC, Geneva, Switzerland.

KAWECKI, T.J. & EBERT, D. (2004) Conceptual issues in local adaptation. *Ecology Letters* **7**, 1225–1241.

KEITH, P., PERSAT, H., FEUNTEUN, E. & ALLARDI, J. (2011) *Les poissons d'eau douce de France.* Muséum National d'Histoire Naturelle and Publications Biotope. Paris and Mèze.

LANGSRUD, O. (2003) ANOVA for unbalanced data: Use Type II instead of Type III sums of squares. *Statistics and Computing*, 163–167.

LEVINE, T.. & HULLETT, C. (2002) Eta squared, partial eta squared, and misreporting of effect size in communication research. *Human Communication Research* **28**, 612–625.

MATTHEWS, B., AEBISCHER, T., SULLAM, K.E., LUNDSGAARD-HANSEN, B. & SEEHAUSEN, O. (2016) Experimental evidence of an eco-evolutionary feedback during adaptive divergence. *Current Biology* **26**, 483–489.

MATTHEWS, B., NARWANI, A., HAUSCH, S., NONAKA, E., PETER, H., YAMAMICHI, M., SULLAM, K.E., BIRD, K.C., THOMAS, M.K., HANLEY, T.C. & TURNER, C.B. (2011) Toward an integration of evolutionary biology and ecosystem science. *Ecology Letters* **14**, 690–701.

MCINTYRE, P.B., FLECKER, A.S., VANNI, M.J., HOOD, J.M., TAYLOR, B.W. & THOMAS, S.A. (2008) Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots. *Ecology* **89**, 2335–2346.

MIMURA, M., YAHARA, T., FAITH, D.P., VÁZQUEZ-DOMÍNGUEZ, E., COLAUTTI, R.I., ARAKI, H., JAVADI, F., NÚÑEZ-FARFÁN, J., MORI, A.S., ZHOU, S., HOLLINGSWORTH, P.M., NEAVES, L.E., FUKANO, Y., SMITH, G.F., SATO, Y.-I., ET AL. (2016) Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evolutionary Applications* **10**, 121–139.

NAKAGAWA, S. & CUTHILL, I.C. (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* **82**, 591–605.

ODLING-SMEE, J., ERWIN, D.H., PALKOVACS, E.P., FELDMAN, M.W. & LALAND, K.N. (2013) Niche construction theory: a practical guide for ecologists. *The Quarterly Review of Biology* **88**, 3–28.

PALKOVACS, E.P., MORITSCH, M.M., CONTOLINI, G.M. & PELLETIER, F. (2018) Ecology of harvest-driven trait changes and implications for ecosystem management. *Frontiers in Ecology and the Environment* **16**, 20–28.

PARMESAN, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**, 637–669.

PINDER, A.. (2001) *Keys to larval and juvenile stages of coarse fishes from fresh waters in the British isles*Freshwater. Biological Association.

R CORE TEAM (2013) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

REY, O., DANCHIN, E., MIROUZE, M., LOOT, C. & BLANCHET, S. (2016) Adaptation to global change: a transposable element–epigenetics perspective. *Trends in Ecology & Evolution* **31**, 514–526.

ROSENBLATT, A.E. & SCHMITZ, O.J. (2016) Climate change, nutrition, and bottom-up and top-down food web processes. *Trends in Ecology & Evolution*.

RUDMAN, S.M., BARBOUR, M.A., CSILLÉRY, K., GIENAPP, P., GUILLAUME, F., HAIRSTON JR, N.G., HENDRY, A.P., LASKY, J.R., RAFAJLOVIĆ, M., RÄSÄNEN, K., SCHMIDT, P.S., SEEHAUSEN, O., THERKILDSEN, N.O., TURCOTTE, M.M. & LEVINE, J.M. (2018) What genomic data can reveal about eco-evolutionary dynamics. *Nature Ecology & Evolution* **2**, 9–15.

SCHOENER, T.W. (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* **331**, 426–429.

THOMPSON, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology & Evolution* **13**, 329–332.

TURCOTTE, M.M., REZNICK, D.N. & DANIEL HARE, J. (2013) Experimental test of an eco-evolutionary dynamic feedback loop between evolution and population density in the green peach aphid. *The American Naturalist* **181**, S46–S57.

WOODWARD, G., EBENMAN, B., EMMERSON, M., MONTOYA, J., OLESEN, J., VALIDO, A. & WARREN, P. (2005) Body size in ecological networks. *Trends in Ecology & Evolution* **20**, 402–409.

YVON-DUROCHER, G., ALLEN, A.P., CELLAMARE, M., DOSSENA, M., GASTON, K.J., LEITAO, M., MONTOYA, J.M., REUMAN, D.C., WOODWARD, G. & TRIMMER, M. (2015) Five years of experimental warming increases the biodiversity and productivity of phytoplankton. *PLoS Biol* **13**, e1002324.

YVON-DUROCHER, G., JONES, J.I., TRIMMER, M., WOODWARD, G. & MONTOYA, J.M. (2010) Warming alters the metabolic balance of ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2117–2126.

Supplementary information for Chapter VI.

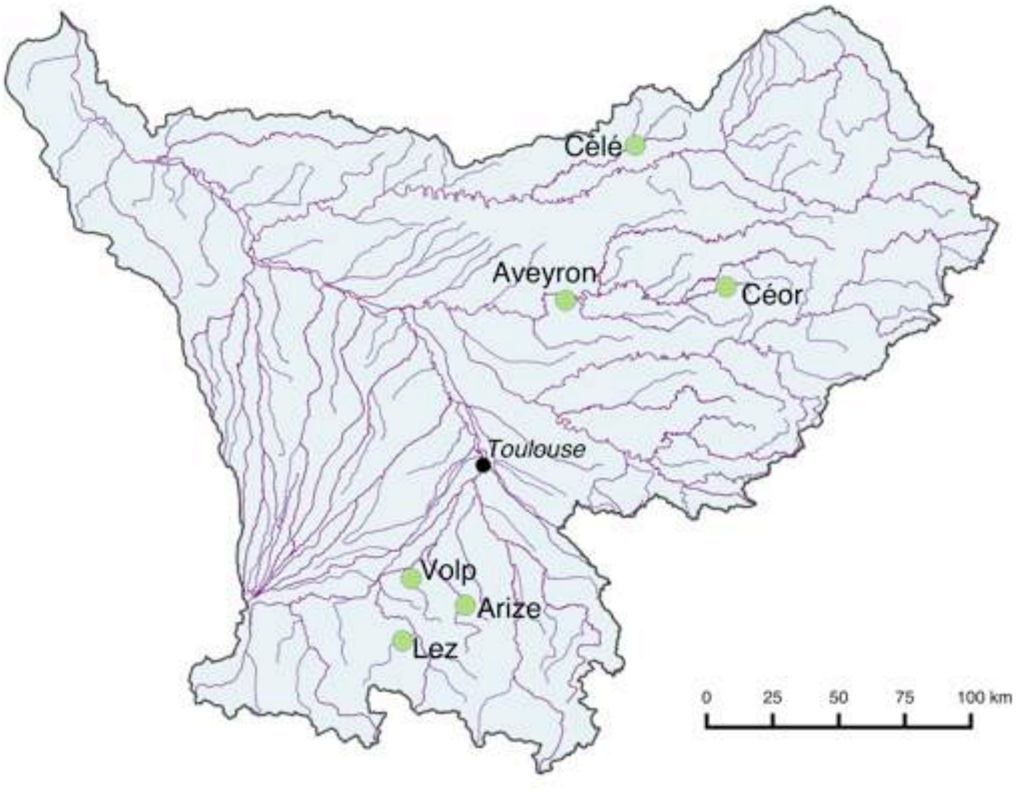

Figure VI.S1. Location of the six populations of adult minnows (*Phoxinus phoxinus*).

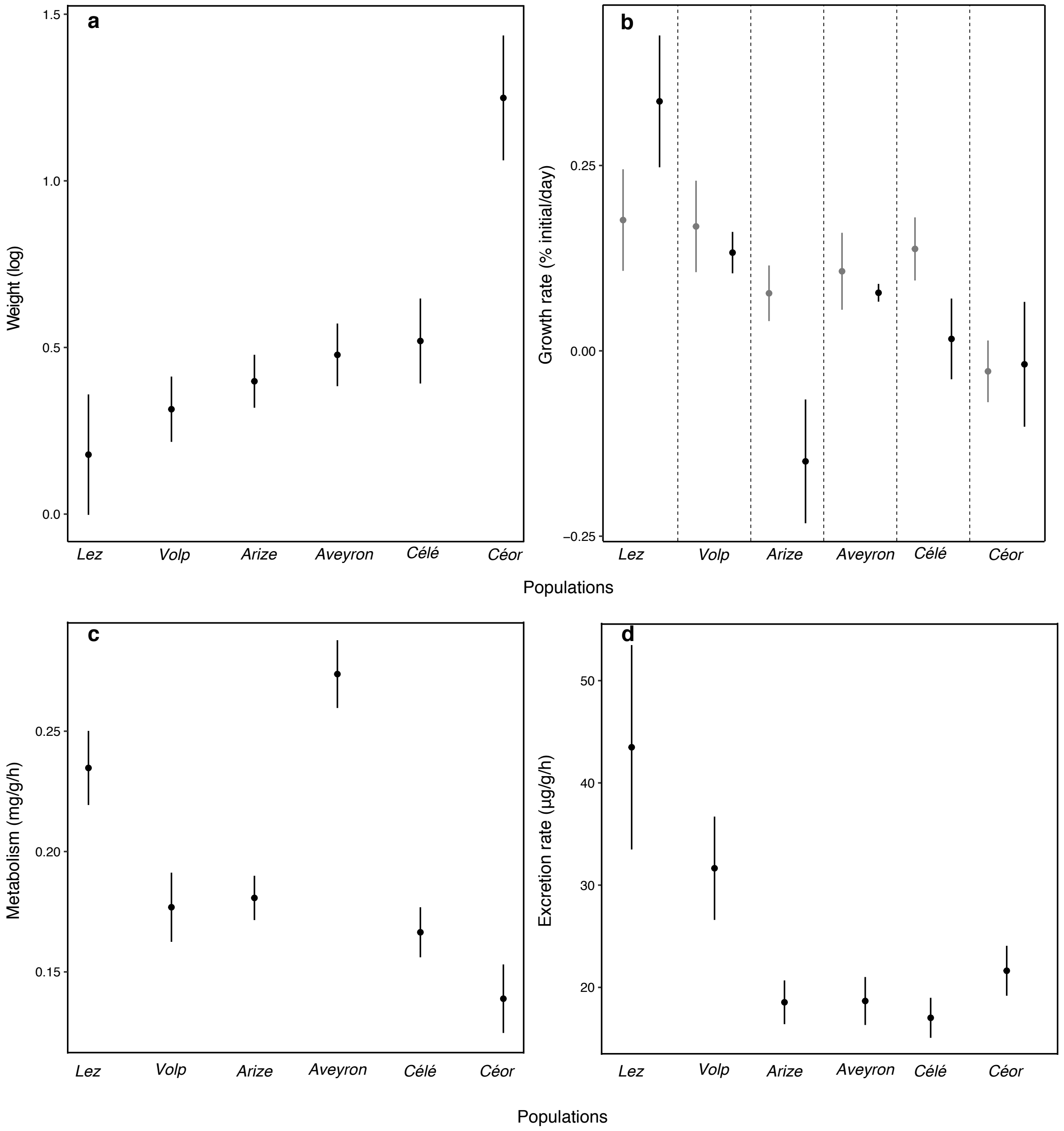

Figure VI.S2. (a) Mean body mass (log-transformed) of fish at the onset of the experiment in function of their origin, error bars represent ± 1 SE. **(b)** Mean growth rate (% of initial mass gain) of adult minnows at the end of the phase 1 in each of the cold (grey) and warm (black) treatment and in function of their origin, error bars represent ± 1 SE. Overall, adult minnows from the different populations differed significantly in their body mass at the onset of the experiment (F = 7.404, d.f = 5, 58, $p < 0.001$). Adult growth rate *during* the experiment depended upon the interaction between their origin and temperature (F = 4.230, d.f = 5, 51, p = 0.002). **(c)** Mean metabolic rate (i.e. oxygen consumption in mg.g^{-1}.h^{-1}) measured on fish from the same population and cohort that fish used in the experiment. To assess the metabolic rate, each fish was individually placed in a custom made metabolic chamber filled with 500 mL of dechlorinated tap water, and the chamber was hermetically sealed. Measurements of oxygen concentration were taken after 10 min, allowing individuals to acclimate, and continuously every five seconds for 50 min with oxygen probes. Chambers were set in a thermoregulated room at 17°C in the dark to lower the stress level. After one hour, fish were gently released in their home tank. Before to start the measurement the individuals were starved for two days to ensure the same starvation level among individuals. Overall, the populations significantly differed in their metabolic rate (F = 14.599, d.f = 5,188 , $p < 0.001$), error bars represent ± 1 SE. **(d)** Mean excretion rate (µg.g^{-1}.h^{-1}) measured on fish from the same population and same cohort that fish used in the experiment. To assess, the excretion rate all individuals were starved for two days prior to the start of the measurement to ensure they have the same starvation level. Individuals were placed in plastic bags containing 500 ml of spring bottled water for 1h at 17°C. Individuals were then removed and 100 ml of water was filtered through a glass microfiber filter (Whatman, GF/C, diameter = 25 mm), and samples were frozen at -20°C. Excretion rate was determined with a high-performance ionic chromatograph (Dionex DX-120). The six populations significantly differed in their ammonium excretion rate (F = 4.695, d.f = 5,175, $p < 0.001$), error bars represent ± 1 SE.

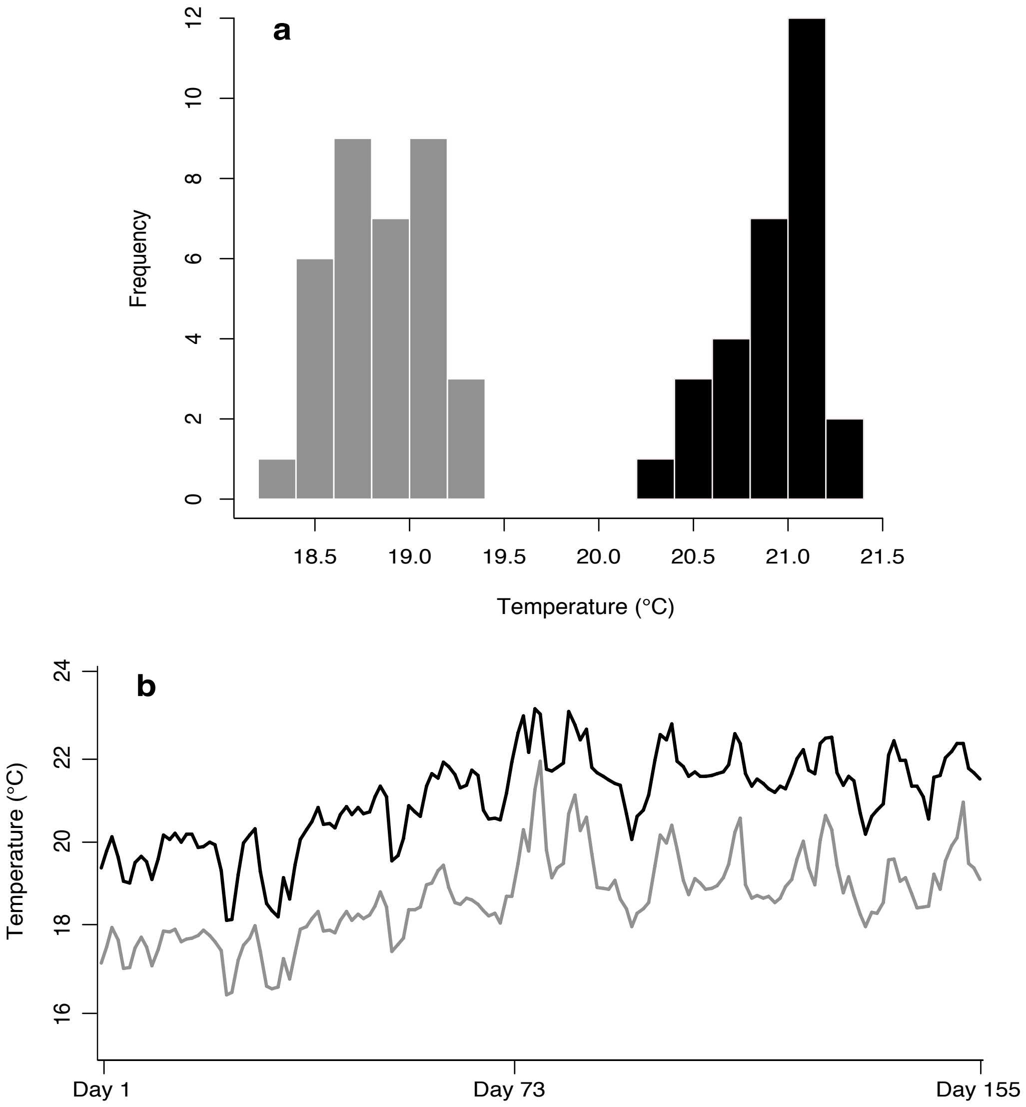

Figure VI.S3. (a) Frequency distribution of mean water temperature measured in each mesocosm from the low and high temperature treatment respectively. Mean water temperatures of mesocosms were significantly different (t = -32.647, d.f = 62, $p < 0.001$) between the low temperature treatment (grey, mean ± SE = 18.83 ± 0.04) and the high temperature treatment (black, mean ± SE = 20.91 ± 0.05). **(b)** Averaged daily water temperature of two randomly chosen mesocosms among the two temperature treatments (low and high temperature treatments in grey and black respectively) illustrating temporal variability of temperature. Water temperature from each tank was continuously surveyed all over the experiment using automatic recorders (Hobo®).

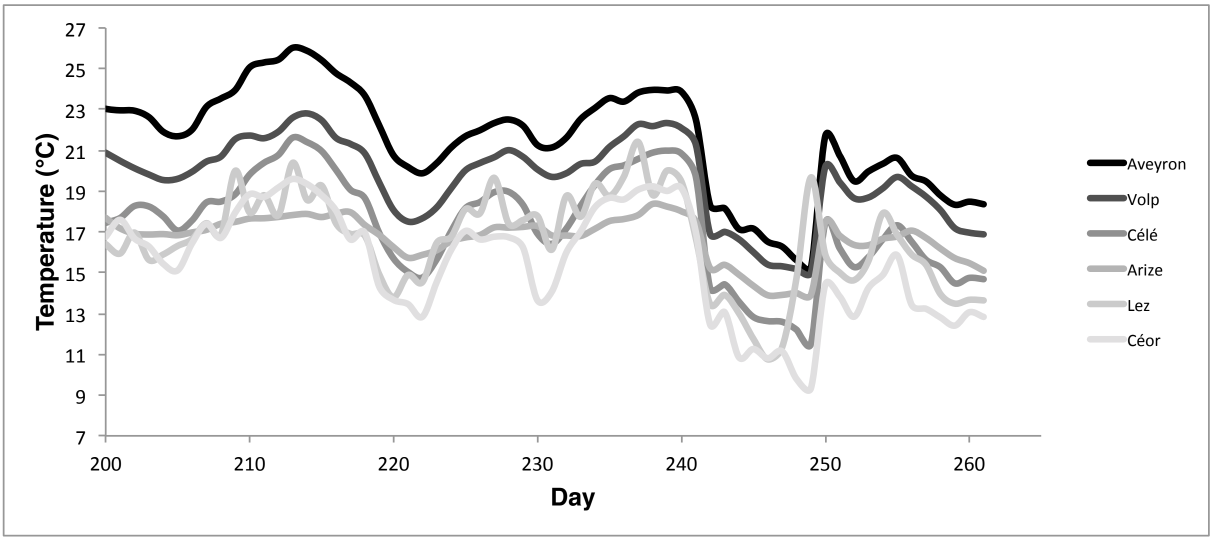

Figure VI.S4. Daily water temperatures for each of the six rivers in which adult minnows (*Phoxinus phoxinus*) were sampled for phase 1 of the experiment. Water temperature was measured continuously in each river at the section where fish were sampled from the 21st of July to the 12th of September 2017 (the growing season) using automatic recorders (Hobo ®).

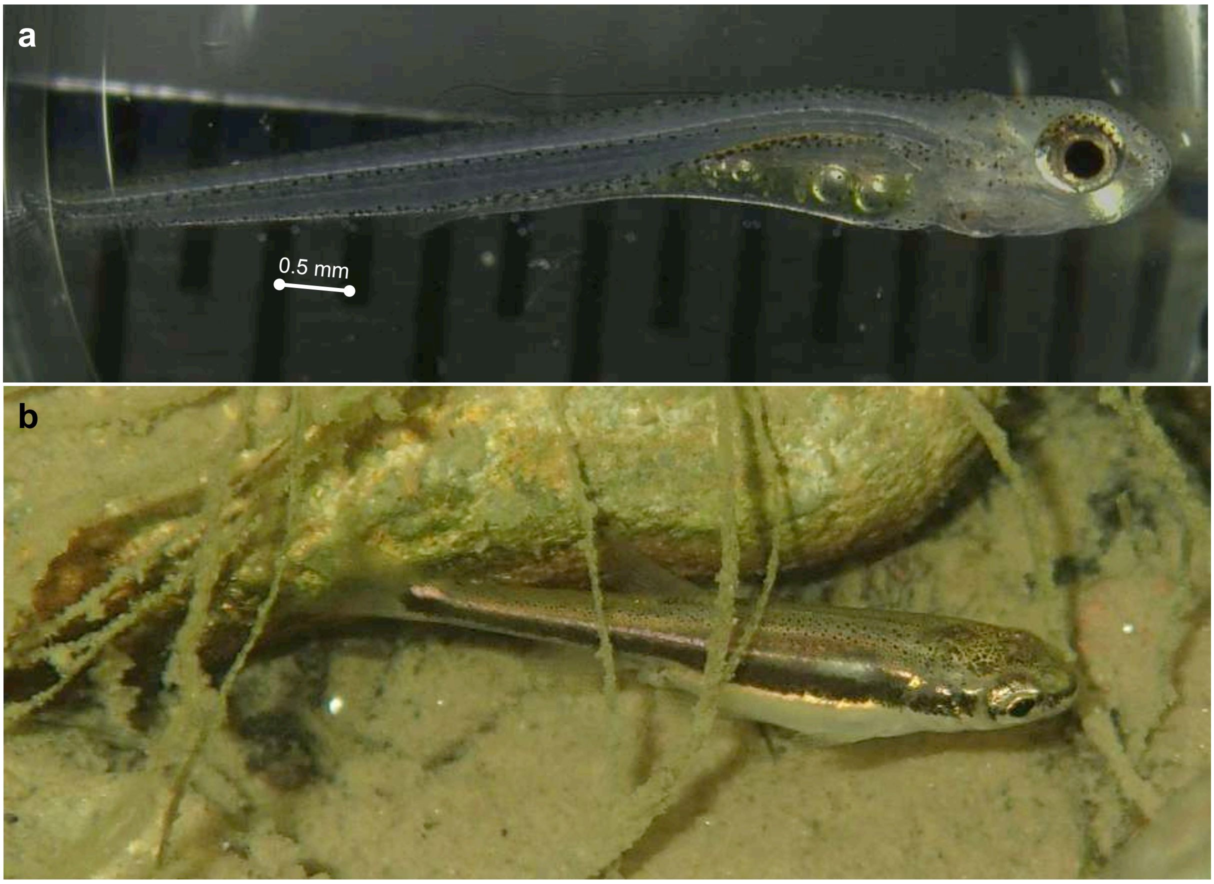

Figure VI.S5. Two weeks old juvenile minnow (*Phoxinus phoxinus,* stage III larvae) at the start of the phase 2 **(a)**, and after 11 weeks at the end of the experiment **(b)**.

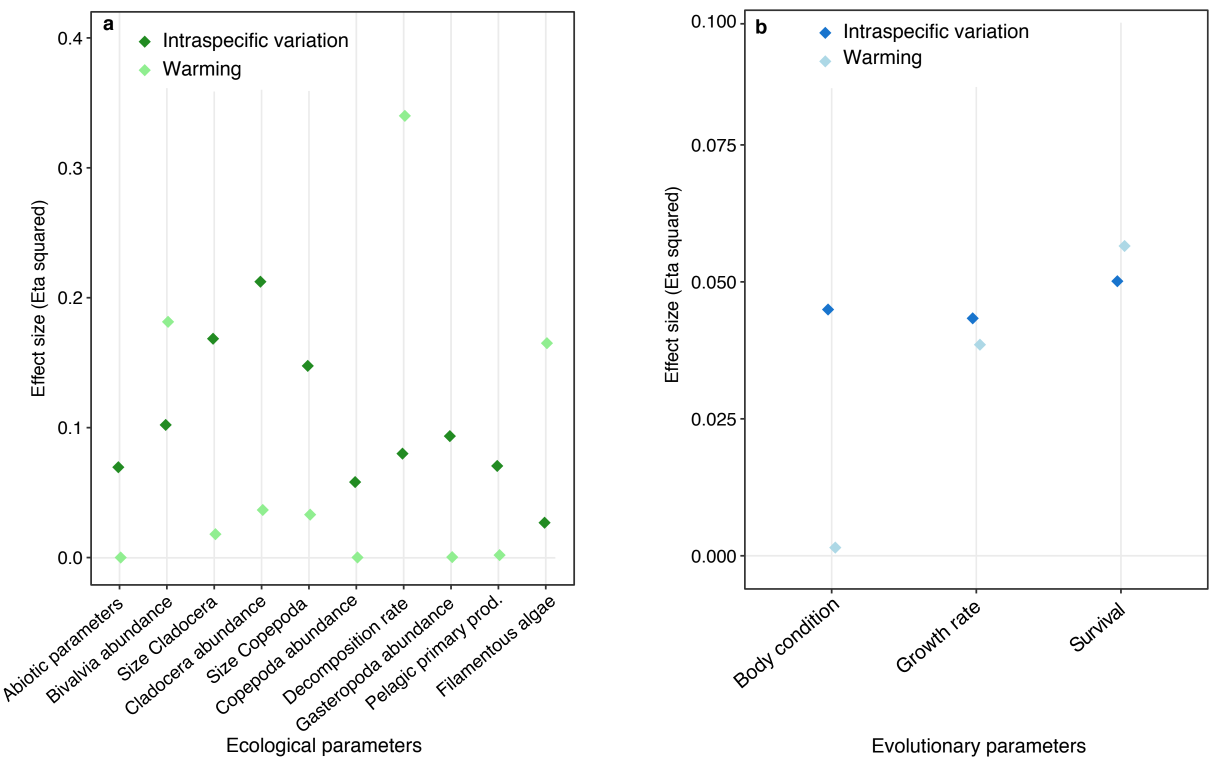

Figure VI.S6. Effect size (Eta squared) of intraspecific variation and warming on ecological **(a)** and fitness **(b)** parameters.

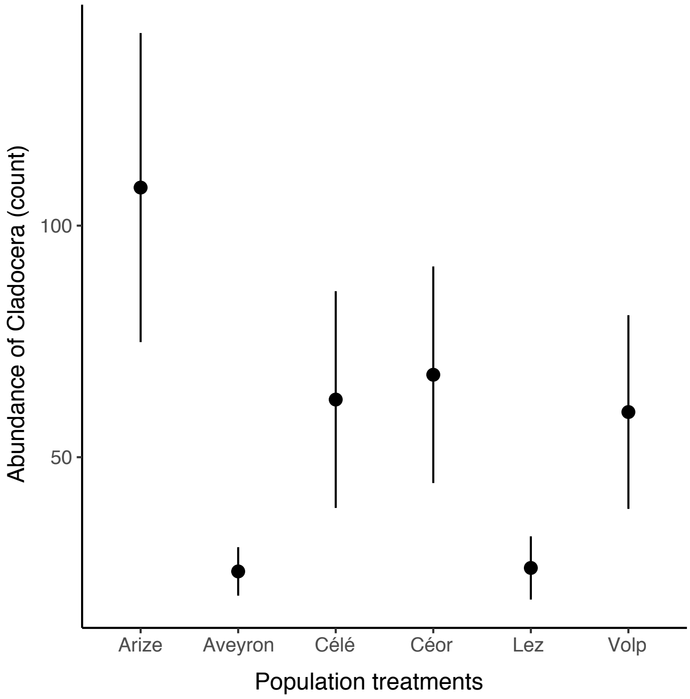

Figure VI.S7. Abundance of Cladocera (count data) remaining in the mesocosms at the end of the phase 1 in function of the population origin of adult minnows (*Phoxinus phoxinus*) at the onset of the experiment. Error bars represent ± 1 SE.

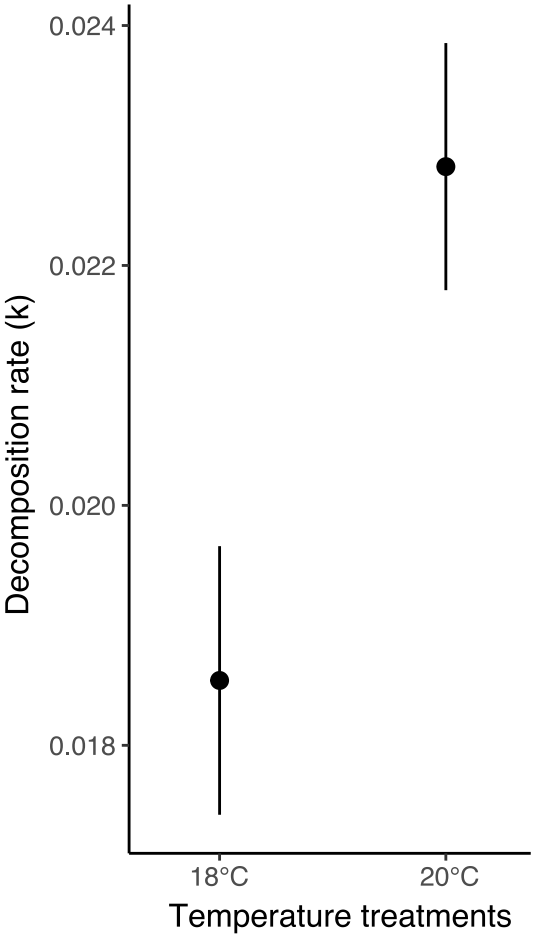

Figure VI.S8. Decomposition rate (k) at the end of the phase 1 in function of the temperature treatment. Error bars represent ± 1 SE.

Chapitre VII.

Intraspecific diversity in consumer populations modifies ecosystem functioning

Allan Raffard[1,2], Julien Cucherousset[3], Murielle Richard[1], Alexandre Garreau[1], Samson Acoca-Pidolle[1], Frédéric Santoul[2], & Simon Blanchet[1]

[1] *CNRS, Université Toulouse III Paul Sabatier, Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UMR-5321, F-09200 Moulis, France.*

[2] *EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France*

[3] *CNRS, Université Toulouse III Paul Sabatier, UMR-5174 EDB (Laboratoire Evolution & Diversité Biologique), 118 route de Narbonne, F-31062, Toulouse, France.*

Manuscript in preparation.

Résumé

Les relations entre la biodiversité et le fonctionnement des écosystèmes (B-FE) ont historiquement été étudiées au niveau interspécifique. L'attention des travaux scientifiques s'est récemment portée sur la diversité intraspécifique. Des études expérimentales ont permis de démontrer que la richesse intraspécifique chez les producteurs primaires pouvait affecter la structure des communautés et le fonctionnement des écosystèmes. Cependant, il n'y a pas encore d'indications que la richesse intraspécifique chez les consommateurs puisse avoir des effets écologiques. Ici, nous avons manipulé la richesse intraspécifique (nombre de populations uniques) et la structure en taille (taille des individus) de populations expérimentales de vairons (*Phoxinus phoxinus*) en mésocosmes. Après 30 semaines d'expérience, la diversité d'invertébrés benthiques augmentait avec la richesse intraspécifique et était affectée par la structure en taille des populations expérimentales. Cette augmentation de la diversité des proies engendrait ensuite une augmentation du taux de décomposition. La richesse intraspécifique impactait aussi la productivité de l'écosystème, une richesse élevée menant à des écosystèmes plus productifs. Les effets de la richesse intraspécifique étaient – dans la plupart des cas – indépendants de la structure en taille des populations expérimentales. Cette étude suggère donc que la richesse intraspécifique module les effets « top-down » des consommateurs en soutenant des communautés plus diversifiées et en modifiant ensuite les processus écosystémiques. La diversité intraspécifique étant constamment menacée et modifiée par les changements globaux, il est crucial d'approfondir nos connaissances sur les relations entre biodiversité intraspécifique et le fonctionnement des écosystèmes.

Abstract

The relationships between biodiversity and ecosystem functioning (BEF) have primarily been studied at the interspecific level. Recent studies have demonstrated that changes in genotypic/phenotypic richness within populations of primary producers (i.e. intraspecific diversity) can affect community structure and ecosystem functioning. However, whether changes in the intraspecific richness of consumers have ecological consequences remains unknown. Here, we manipulated intraspecific richness (number of unique populations) and size structure (individual size) of experimental populations of European minnows (*Phoxinus phoxinus*) in a mesocosm experiment. After 30 weeks, we found that the diversity of benthic prey invertebrates significantly increased with increasing intraspecific richness, and was also modulated by the size structure of experimental populations. This increase in prey diversity subsequently increased decomposition rate. Intraspecific richness also led to higher ecosystem productivity. The effects of intraspecific richness were – in most cases – independent from the size structure of the assemblages. Overall, our study suggests that the loss in intraspecific diversity in consumers can lead to detrimental top-down effects on both prey diversity and key ecosystem processes.

Introduction

Biodiversity is strongly affected by human disturbances, and this has major consequences for ecosystem functioning. The effects of changes in biodiversity on ecosystem functioning (BEF) have been intensively investigated, and studies demonstrated that changes in species composition within communities can ultimately alter ecosystem services (Naeem *et al.*, 2009; Schmitz *et al.*, 2014; Duffy *et al.*, 2016). In this context, within-species diversity is the primary facet of biodiversity being modulated by global changes (Parmesan, 2006). Differences in intraspecific diversity has recently been acknowledged to be an essential predictor of ecological dynamics (Chapter III, Des Roches *et al.*, 2018).

Genotypic richness within plant populations can affect the structure of surrounding communities and ecosystem processes, generating what has been called *intraspecific BEF* ('iBEF', Chapter III, Crutsinger *et al.*, 2006; Koricheva & Hayes, 2018). Thereby, the loss of genotypes within populations can decrease ecosystem process rates and species diversity because of the loss of positive interactions among individuals, such as facilitation (Johnson, Lajeunesse, & Agrawal, 2006; Fridley & Grime, 2010). While iBEF have now been widely explored in primary producers (Chapter III, Koricheva & Hayes, 2018), fewer studies have focused on iBEF generated by consumers species through top-down effects (see for instance Hargrave, Hambright, & Weider, 2011). This is despite the fact that consumer species are important for ecological dynamics by exerting strong control on lower trophic levels (Terborgh & Estes, 2010) and that human pressures strongly influence their intraspecific diversity (Daufresne, Lengfellner, & Sommer, 2009; Palkovacs *et al.*, 2012, 2018).

The ecological effects of intraspecific richness are likely dependant of functional complementarity among the individuals composing the populations (Hughes *et al.*, 2008). In consumers, body size is one of the most integrative trait for explaining functional differences among individuals (Rudolf & Rasmussen, 2013a). Indeed, body size is associated with key functional processes such as food acquisition and nutrient cycling, which can influence functional complementarity among individuals and then community and ecosystem dynamics (Woodward *et al.*, 2005; Hildrew, Raffaelli, & Edmonds-Browns, 2007; Rudolf & Rasmussen, 2013b; Rudolf *et al.*, 2014). The size structure of individuals within a population could hence mediate the ecological effects of richness by determining functional interactions among individuals, such as resource partitioning. First attempts manipulating variance in body size within experimental populations have led to contrasting results (Ingram, Stutz, & Bolnick, 2011; Carlson & Langkilde, 2017) and there is still no clear evidence that functional complementarity in consumer populations can exert a top-down control over community structure and ecosystem functioning.

Here, we quantified the ecological effects of changes in intraspecific richness, and in the size structure of experimental populations to test whether functional complementarity among individuals could mediate the effects of intraspecific richness. In mesocosms, we manipulated intraspecific richness (number of unique populations that individuals originated from) and the size structure (mean and variance in individuals body mass) of experimental populations of European minnows (*Phoxinus phoxinus*). We expected higher richness to support higher diversity of prey community because of complementary such as resource partitioning, and to increase subsequently the rate of ecosystem processes. We further expected that the size structure could modulate previous relationships either through a biomass effect (i.e. large-bodied and small-bodied treatments, Rudolf *et al.*, 2014) or by enhancing the complementarity effect (in the mix treatment, Figure VII.1).

Material and methods

Model species

We carried out this study using the European minnow (*Phoxinus phoxinus*) as a model species. This is an abundant species in Western Europe living in relatively cold water (summer water temperature generally lower than 24°C) including mountains lakes, small rivers at intermediate altitude and mountain streams (Keith *et al.*, 2011). It is a small-bodied cyprinid fish species (<12 cm long, 4-8 cm long as an adult in general) with a generalist diet composed of small invertebrates, algae or zooplankton (Frost, 1943; Collin & Fumagalli, 2011). Populations of European minnows have been shown to display different genetic and phenotypic richness (Fourtune *et al.*, 2018), and previous works revealed that different populations can strongly affect the prey community structure and ecosystem functioning (Chapter VI). This suggests that unique populations are functionally different and display different role in their environment.

We selected ten populations in the Dordogne-Garonne basin based on *a priori* knowledge to maximise evolutionary and functional differentiations among populations (Chapter VI, Fourtune *et al.*, 2018) (Figure VII.S1). Specifically, we sampled five populations containing small adults (mean body mass ± standard error (SE) = 1.03 g ± 0.02) and five populations containing large adults (mean body mass ± SE = 3.06 g ± 0.07) (Figure VII.S2a).

These differences in the body mass of adults have been shown to be related to pressures from the local environment such as predator densities and mean water temperature (Chapter IV). In September 2017, we sampled fish in each river using electrofishing. A 200 m section was sampled to collect ~70 adults within the size range of the population, assessed visually. We then picked 30-50 individuals to ensure that sampled fish were representative of the populations. Electrofishing were done under the authorization of local authorities (Arrêté Préfectoral from the Direction départementale des territoires of French departments Ariège, Haute-Garonne, Tarn, Aveyron, Tarn-et-Garonne, Lot).

Mesocosm experiment

In October 2016, we set 24 outdoor mesocosms. They were distributed in 10 blocks and 8 rows, depicting the distance from the nearest river (< 200 m), and were used to control for potential block and river effects (e.g. aerial colonization). They were filled with 900 L of water, and 3 cm of gravel from 1 to 10 cm diameters. We added nutrients to the mesocosms using 10 mL of solution containing nitrogen and phosphorus (ratio N:P:K = 3.3:1.1:5.8) in October 2016. Each mesocosm was then inoculated twice with 200 mL of a concentrated solution of phytoplankton and 200 mL of concentrated solution of zooplankton collected from a unique lake nearby the laboratory (Lake Lamartine, France 43°30'21.5"N, 1°20'32.7"E) in October 2016 and May 2017 respectively. Finally, in May 2017, we introduced three adults pond-snails (Lymnaeidae) and ten adults isopods (Asellidae) in each tank. Mesocosms were let uncovered to allow natural colonization by other invertebrates until the start of the experiment.

In October 2017, eight fish were introduced in each mesocosm, which were assigned to one of six treatments according to a full-factorial design with richness (two levels, high and low richness) and size structure (three levels, large, small, and large and small individuals) as the main factors (Figure VII.1). We manipulated the origin of fish present in mesocosm to make experimental populations differing in their richness. We aimed at testing explicitly the effects of richness, while minimizing the effects of population identity; each replicate of each treatment of richness contained a different assemblage of populations, and monoculture for each population was not included in the experiment. For the richness factor, the two levels were: (i) a *low richness* level in which individuals were sourced from two distinct populations, and (ii) a *high richness* level in which individuals were sourced from four distinct populations (Figure VII.1). The richness treatments were crossed with three levels of the size structure factor. This consisted in explicitly manipulating the body mass (an important functional trait, Rudolf *et al.*, 2014) of the individuals present in the mesocosms, hence experimental populations contained either (i) *large*, (ii) *small,* or (iii) small and large individuals (*mix*) (Figure VII.1 see also Table VII.S1 for details on the different experimental populations).

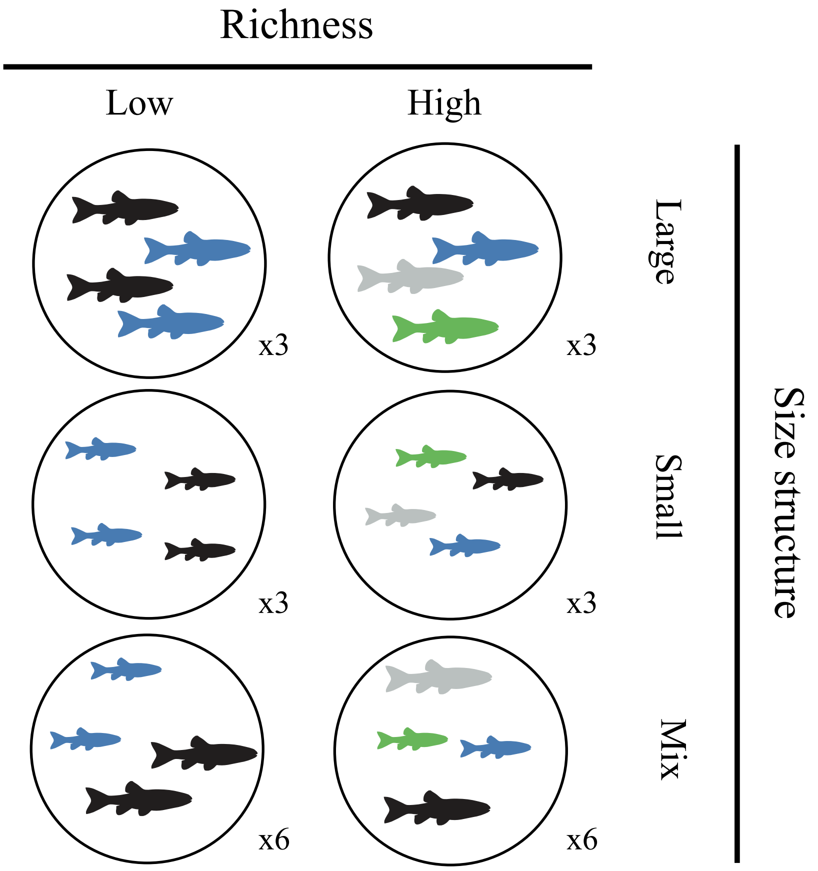

Figure VII. 1. Summary of the experimental design used to test the ecological effects of intraspecific richness and size structure. Colour of symbol denotes population origin of individuals, and the size of symbols denotes the individual phenotype (large or small individuals). Note that eight fish were introduced in each mesocosm.

Tanks were daily checked for mortality, which was rare over the course of the experiment but the week before the ending of the experiment (due to higher temperatures in the tanks), which led us to end the experiment. Therefore, after 30 weeks (i.e. May 2018), we measured several ecological parameters to assess the potential treatment effects on community structure and ecosystem functioning.

- Zooplankton community was assessed by filtering 5 L of water through a 200 µm sieve. Samples were conserved in a 70% ethanol solution and subsequently identified to the order or family levels, including Cyclopoida, Calanoida, Daphniidae, Chydoridae and Bosminidae. The diversity of zooplankton was calculated as the Simpson's diversity (*D-zoo*) representing the probability that two randomly chosen individuals belong to different clades. *D-zoo* was calculated as $1 - \frac{\sum N_i * (N_i - 1)}{N_{tot} * (N_{tot} - 1)}$, where N_{tot} was the total number of sampled individuals, and N_i the number of sampled individuals for each group (Simpson, 1949; Lande, 1996).

- Benthic invertebrates were collected from the mesh bags used to measure decomposition rates (*see below*), conserved in a 70% ethanol solution, and identified as Asellidae, Diptera, Gastropoda, Ephemeroptera, Plecoptera, Odonata, Copepoda, Cladocera, and Ostracoda. The diversity of benthic invertebrates was calculated as the Simpson's diversity (*D-inv*).

- Decomposition rate was measured by quantifying the mass loss of black poplar (*Populus nigra*, a dominant riparian tree in southern France) abscised leaves (Alp *et al.*, 2016). The 7th March 2018, 4 g of air-dried leaves were put in each mesocosm within a coarse mesh (1 x 1 cm) bag. At the end of the experiment, the remaining leaf material was removed from the mesocosms, rinsed with tap water, oven dried at 60°C for three days and weighed to the nearest 0.001 g to assess the loss of biomass. The decomposition rate was calculated as $k = -\frac{ln\,(X)}{t}$ (Alp *et al.*, 2016), where X is the proportion of litter remaining and t is the elapsed time in days.

- Nutrient composition of water was measured as the dissolve concentration of NH_4^+ and PO_4^{3-} (hereafter referred to as N and P). We filtered 50 mL of water in each mesocosm through a glass microfibre filter (Whatman, GF/C, diameter 1⁄4 25 mm) and samples were frozen at -20°C. N and P (µg.L^{-1}) were determined using a high-performance ionic chromatograph (Dionex DX-120).

- Pelagic algae stock was measured as the chlorophyll-a concentration (µg.L^{-1}) in the water column using a multiparameters probe (OTT, Hydrolab DS5®). Five measurements were taken in each mesocosm and subsequently averaged for the analyses.

- Gross primary production (GPP), net primary production (NPP) and respiration (R) were calculated using changes in oxygen concentration in the mesocosms. Oxygen concentration was measured, using a multi-parameter probes (OTT, Hydrolab DS5®), at sunrise (t_0, minimal oxygen concentration), sunset (t_1, maximal oxygen concentration) and the following sunrise (t_2, minimal oxygen concentration). NPP was calculated as t_1-t_0, R as t_1-t_2 and GPP as NPP+R. Since these three parameters were highly correlated ($r > 0.82$), we summarized them into a Z score. GPP, NPP and R were scaled to the mean (mean of 0 and variance of 1) and averaged together to obtain an ecosystem productivity score.

Statistical analyses

Prior to analysis, the pelagic algae stock (i.e. the chlorophyll-a concentration) and the concentration of N and P were log-transformed to approximate normality. After analyses of outliers, we removed one mesocosm from final analyses that displayed (for unknown reasons) evident outliers for several variables. Analyses were hence run on 23 replicates.

To assess the causal links among intraspecific richness, size structure and community structure and ecosystem functioning, we ran mixed effects linear models (LMM). We ran one model for each ecological parameter measured, leading to a total of seven models (Table VII.1). The models with the diversity indices (*D-inv and D-zoo*) as dependent variables included the richness and the size structure as explicative variables. The models with N and P concentrations as dependent variables included richness, size structure, diversity of benthic invertebrates, diversity of zooplankton, and decomposition rate as explicative variables. The model with the decomposition rate as dependent variable included the diversity of benthic invertebrates as explicative variable. The model with the pelagic algae stock as dependent variable included the N and P concentrations, and the diversity of zooplankton as explicative variables. The model with the ecosystem productivity score as dependent variable included richness, size structure, diversity of benthic invertebrates, diversity of zooplankton, decomposition rate, N and P concentrations, and pelagic algae stock as explicative variables. In each model in which intraspecific richness and size structure were included, we also added the interaction term between factors. This interaction was removed when non-significant because it prevents the interpretation of simple terms. The mortality rate of fish during the experiment (mean ± standard error (SE) = 0.22 ± 0.01) was included as a fixed effect so as to control for a potential effect of final density on ecological dynamics. To control for the disposition of the tanks during the experiment, a block effect and distance from the river were added as random terms. Finally, as multiple testing increases the probability of Type I error, the *p*-values were adjusted for false discovery (Benjamini & Hochberg, 1995). All statistical analysis were run using R software (R Core Team, 2013) and LMM were run using the R-package lme4 (Bates *et al.*, 2014).

Table VII.1. Description of the biological hypotheses used to construct a set of causal models linking the ecological parameters measured at the end of the experiment and the treatments of richness and size structure. Each ecological parameter was set as a dependent variable, and the predictors were set as explicative variables. Overall, seven mixed linear models were run.

Ecological parameters	Predictors	Biological hypotheses	References
Diversity of benthic invertebrates & Diversity of zooplankton	Intraspecific richness	Higher prey diversity in richer treatments because of resource partitioning among genotypes.	Johnson *et al.*, 2006; Carlson & Langkilde, 2017
	Size structure	Difference of diet between small and large individuals.	
Nutrient (N and P)	Intraspecific richness	Faster nutrient turnover in richer populations.	McIntyre *et al.*, 2007; Schmitz, Hawlena, & Trussell, 2010
	Size structure	Body mass increases excretion rate and nutrient concentration.	
	Diversity of benthic invertebrates & Diversity of zooplankton	Nutrient turnover increased by biodiversity.	McIntyre *et al.*, 2007
	Decomposition rate	Higher nutrient release by faster decomposition rate.	Gessner, Chauvet, & Dobson, 1999
Decomposition rate	Diversity of benthic invertebrates	Resource partitioning and facilitation increased by invertebrate diversity should increase decomposition rate.	Gessner *et al.*, 2010
Pelagic algae stock	Diversity of zooplankton	Resource partitioning and facilitation enhanced by biodiversity should lead to a lower algae stock.	Hargrave *et al.*, 2011
	N & P	Nutrient limitation for phytoplankton growth.	Vanni, 2002
Ecosystem productivity score	Intraspecific richness & Size structure	Higher productivity in richer and heavier populations because of metabolic effects enhancing carbon turnover.	Brown *et al.*, 2004; Schmitz *et al.*, 2014
	Diversity of benthic invertebrates and of zooplankton	High biodiversity leads to more productive system.	Downing & Leibold, 2002
	N & P	Nutrient concentration affects positively ecosystem productivity.	Vanni, 2002
	Decomposition rate	Positively linked to ecosystem respiration.	Gessner *et al.*, 1999
	Pelagic algae stock	Quantity of phytoplankton positively influences ecosystem productivity.	

Results

We found that both intraspecific richness and the size structure of experimental populations affected significantly prey community structure (Figure VII.2, Table VII.2). Specifically, the diversity of benthic invertebrates was higher in the *high richness* treatment (mean *D-inv* ± SE = 0.64 ± 0.04) than in the *low richness* treatment (*D-inv* ± SE = 0.53 ± 0.03, $\chi^2 = 7.067$; d.f = 1, $p = 0.027$; Figure VII.3a). The size structure was also important since mesocosms with *large* or *small* individuals led to a higher diversity of benthic invertebrates than mesocosms with *mix* individuals ($\chi^2 = 9.728$, d.f = 2, $p = 0.027$; Figure VII.3a). The diversity of benthic invertebrates was subsequently and positively related to the decomposition rate ($\chi^2 = 14.441$, d.f = 1, $p = 0.001$; Figure VII.3b) leading to an indirect effect of intraspecific richness and size structure on decomposition rate. The diversity of zooplankton (*D-zoo*) was affected by the interaction between intraspecific richness and the size structure ($\chi^2 = 24.199$, d.f = 2, $p < 0.001$; Figure VII.3c). The diversity of zooplankton was higher in the high richness treatment, excepted when populations were composed only with large individuals (Figure VII.4, Table VII.2), suggesting that, in this case, the effect of intraspecific richness depended on the size of individuals.

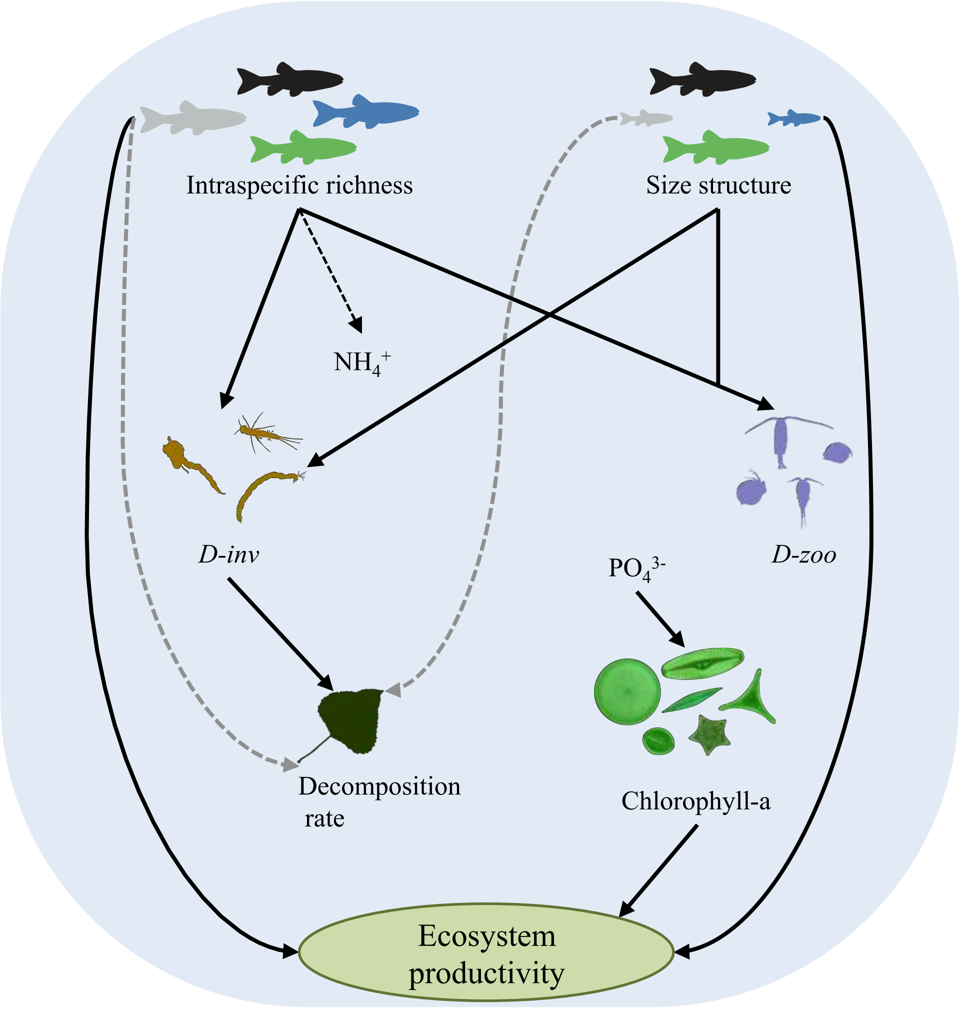

Figure VII. 2. Causal relationships among intraspecific richness, size structure of experimental populations and community and ecosystem parameters. Plain arrows represent significant relationships ($\alpha < 0.05$) and the black dashed arrow indicates a trend ($0.05 < \alpha < 0.10$). Grey arrows denote the indirect effects of initial treatments on decomposition rate.

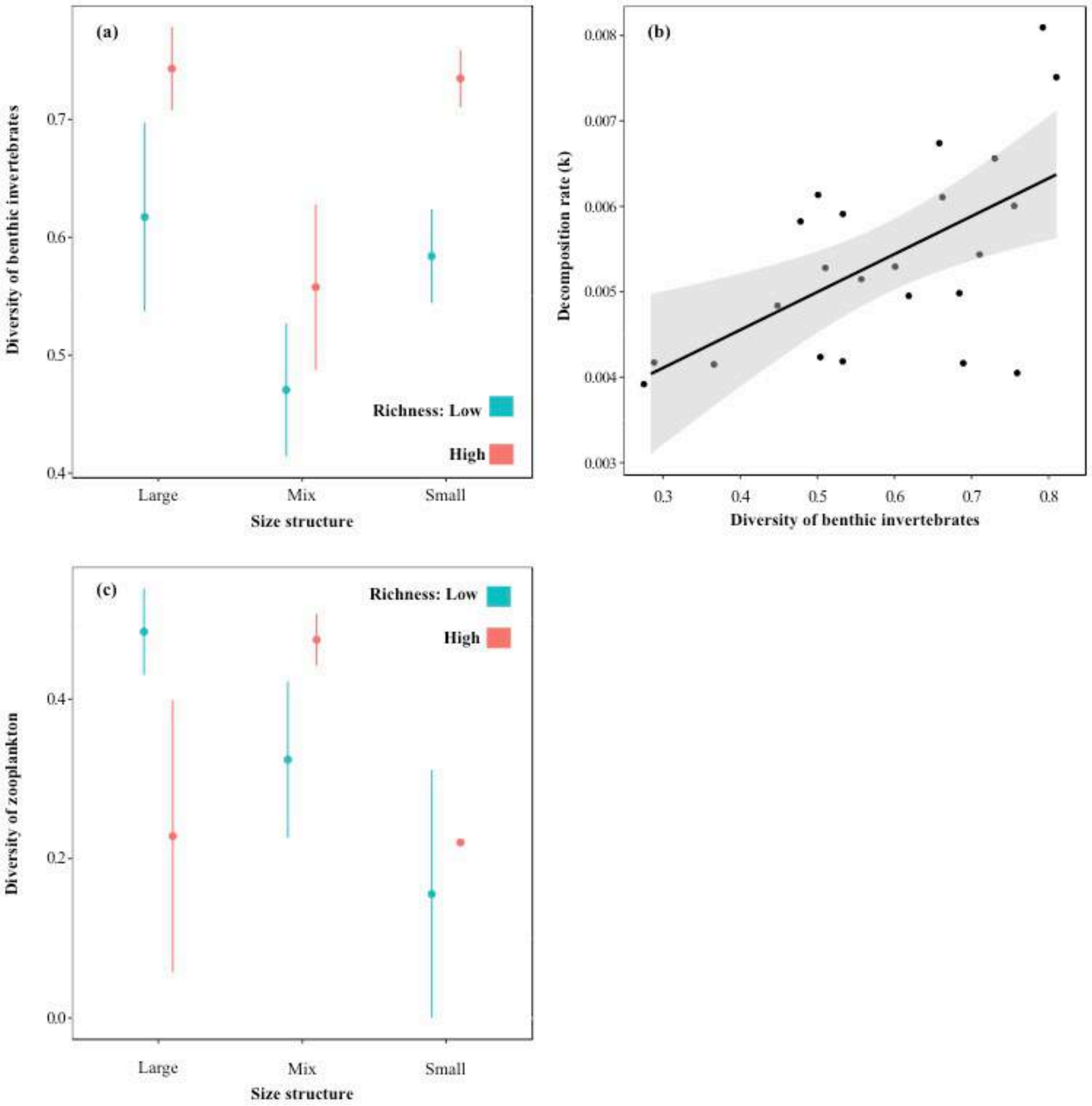

Figure VII.3. Relationships between **(a)** the diversity of benthic invertebrates (*D-inv*) and intraspecific richness and size structure; between **(b)** the diversity of benthic invertebrates and decomposition rate; and between **(c)** the diversity of zooplankton (*D-zoo*) and intraspecific richness and size structure. Error bars in (a) and (c) represent ± 1SE, and grey shadow in (b) represent 95% CI.

Intraspecific richness and the size structure also affected directly ecosystem functioning (Figure VII.2). The N concentration tended to be positively affected by intraspecific richness ($\chi^2 = 5.038$, d.f = 1, $p = 0.070$) but the former was not related to any other ecosystem processes (Figure VII.2). The P concentration led to a significant increase of the pelagic algae stock ($\chi^2 = 13.699$, d.f = 1, $p = 0.001$). Finally, the ecosystem productivity score was significantly and positively related to intraspecific richness ($\chi^2 = 8.282$, d.f = 1, $p =$

0.017), high intraspecific richness leading to more productive ecosystems (Figure VII.4a). It was also affected by the size structure of experimental populations, larger individuals increasing the ecosystem productivity score ($\chi^2 = 8.839$, d.f = 2, $p = 0.037$; Figure VII.4a). Finally, the pelagic algae stock strongly influenced the ecosystem productivity ($\chi^2 = 41.315$, d.f = 1, $p < 0.001$; Figure VII.4b). Overall, we detected an effect of the mortality rate solely on the pelagic algae stock ($\chi^2 = 16.522$, d.f = 1, $p < 0.001$, Table VII.2).

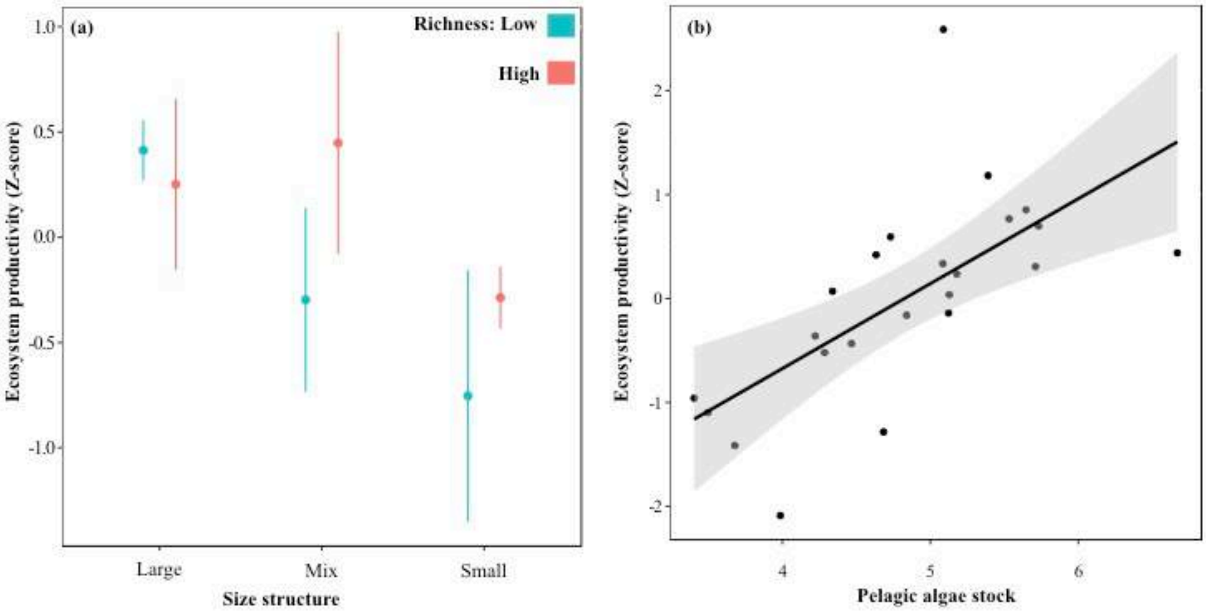

Figure VII.4. Relationships between **(a)** the ecosystem productivity (Z-score among GPP, NPP and R) and intraspecific richness and size structure; and between **(b)** the ecosystem productivity and pelagic algae stock ($\mu g.L^{-1}$). Error bars in (a) represent ± 1SE, and grey shadow in (b) represent 95% CI.

Table VII.2. Results of the mixed effect linear models explaining the relationships among intraspecific richness, size structure and ecological parameters. Significant *p*-values are displayed in bold, and χ^2 and degree of freedom are shown into brackets.

Response	Effect	*p*-value	
Diversity of benthic invertebrates	**Richness**	**0.027**	(7.067, 1)
	Size structure	**0.027**	(9.728, 2)
	Mortality	0.350	(1.600, 1)
Diversity of zooplankton	**Richness**	**0.013**	(9.032, 1)
	Size structure	**< 0.001**	(27.196, 2)
	Richness*size structure	**< 0.001**	(24.199, 2)
	Mortality	0.647	(0.324, 1)
N	Richness	0.070	(5.038, 1)
	Size structure	0.299	(3.578, 2)
	Decomposition rate	0.461	(0.863, 1)
	Diversity of benthic invertebrates	0.424	(1.071, 1)
	Diversity of zooplankton	0.294	(2.018, 1)
	Mortality	0.528	(0.651, 1)
P	Richness	0.424	(1.021, 1)
	Size structure	0.413	(2.638, 2)
	Decomposition rate	0.275	(2.203, 1)
	Diversity of benthic invertebrates	0.960	(0.005, 1)
	Diversity of zooplankton	0.707	(0.213, 1)
	Mortality	0.275	(2.273, 1)
Decomposition rate	**Diversity of benthic invertebrates**	**0.001**	(14.441, 1)
	Mortality	0.356	(1.506, 1)
Pelagic algae stock	Diversity of zooplankton	0.549	(0.565, 1)
	P	**0.001**	(13.699, 1)
	N	0.417	(1.157, 1)
	Mortality	**< 0.001**	(16.522, 1)
Ecosystem productivity score	**Richness**	**0.017**	(8.282, 1)
	Size structure	**0.037**	(8.839, 2)
	Pelagic algae stock	**< 0.001**	(41.315, 1)
	Decomposition rate	0.960	(0.002, 1)
	N	0.160	(3.504, 1)
	P	0.180	(3.078, 1)
	Diversity of zooplankton	0.168	(3.301, 1)
	Diversity of benthic invertebrates	0.852	(0.062, 1)
	Mortality	0.647	(0.321, 1)

Discussion

Our study extents the scope of iBEF relationships showing that modifying intraspecific diversity in consumer species can modify the top-down control of ecosystems. We show that changes in intraspecific diversity, both through a modification of richness and individual size within populations, affect community structure and ecosystem functioning leading to iBEF relationships. Specifically, increasing intraspecific richness from two to four entities supports higher diversity of prey community and increases the rates of two major ecosystem processes. Interestingly, intraspecific richness induces iBEF relationships (i.e. richness affects community and ecosystem), and subsequently BEF relationships through the effect of community structure on ecosystem, which would be important to consider when predicting the effects of intraspecific diversity on ecosystem functioning. Community and ecosystem consequences of changes in the size structure of experimental populations were also significant, and acted - in most cases - independently from the population richness. This indicates that cryptic functional traits, other than body size, were involved and ecologically important.

We observed that intraspecific richness supported higher prey community diversity, mainly for benthic invertebrates, suggesting richness of consumers populations can control the diversity of lower trophic levels. This was likely because of resource partitioning among the individuals composing the experimental populations, which is expected to be higher in the higher intraspecific richness treatments (Duffy, 2002; Johnson *et al.*, 2006). Individuals from different natural populations can differ in their trophic selectivity, and filled different ecological niches. Thereby, in the high richness treatment individuals forage on variable items regulating the abundance of each taxonomic group allowing a higher diversity (Duffy, 2002). This community effect was independent of individual body size suggesting that intraspecific functional diversity can stand in other traits than body mass. These ‘phantoms’ traits, such as metabolic rate or behaviour, could induce different energetic needs and diet and ultimately ecological consequences (Brown *et al.*, 2004; Careau & Garland, 2012; Rosenblatt & Schmitz, 2016). Overall, the top-down control of intraspecific richness on community structure likely holds on trophic mechanisms, and measuring individuals diet of individuals in such experiments would allow understanding precisely how these community effects arose.

Our results further show that this effect of intraspecific richness on community diversity can subsequently affect ecosystem functioning. As such, an indirect effect was driven by a classical BEF relationship between community diversity and decomposition rate

(Hooper *et al.*, 2005; Gessner *et al.*, 2010). Specifically, intraspecific richness enhanced benthic invertebrate diversity with a magnitude strong enough so that this change in community diversity led to faster litter decomposition rate. The higher decomposition rate of organic matter is likely produced by higher consumption efficiency through trophic complementarity among clades of invertebrates in diverse community (Gessner *et al.*, 2010). Invertebrates community with a high diversity probably harboured a high functional diversity (Cadotte, Carscadden, & Mirotchnick, 2011), and focusing the functional type of invertebrates might allow a more precise understanding of this link. Not only intraspecific richness affects indirectly decomposition rate through changes in community diversity, but it also affects directly ecosystem productivity. This effect is less straightforward than others and probably involves metabolic mechanisms. Richer assemblages are expected to have a higher resource acquisition (through partitioning), which could induce a higher nutrient and carbon immobilization contributing to biomass production (Duffy *et al.*, 2016). Growth rate might then affect oxygen uptake by fish and ultimately ecosystem productivity (Brown *et al.*, 2004). This effect of intraspecific richness was less evident in populations composed of large-bodied size fish (Figure VII.4), probably because - in general - larger fish do not exert a high growth rate, and already consume large amount of oxygen to maintain basal metabolic rate. Alternatively, this effect might arise from unmeasured indirect effects mediated by other ecological parameters. Overall, these results echo those reported at the community level and those manipulating richness within primary producer species (Downing & Leibold, 2002; Crutsinger *et al.*, 2006), and highlight the importance of richness within consumer species for maintaining ecosystem processes.

Finally, we found independent ecological effects of the size structure of the experimental populations, and interestingly, two types of effects were observed. First, the assemblage type was important as the mix treatment differed from the two others (large and small) regarding the effect on benthic community diversity. Contrary to our expectation of functional complementarity enhanced in experimental populations with large and small individuals, they led instead to a decrease of invertebrate diversity compared to assemblages with either large or small individuals. We can rather speculate that complex interactions among individuals with different size, perhaps dominance or behavioural changes, which subsequently modulate the community effects of the populations. Second, the size structure treatments being correlated with body mass (Figure VII.S2c), it can also induce a biomass effect (Rudolf *et al.*, 2014). Indeed, body mass is an important functional traits varying within species that can affect a wide range of ecological processes (Rudolf & Rasmussen, 2013a, 2013b). Here, ecosystem productivity was enhanced in the presence of large individuals. Assemblages with high biomass should consume high quantity of oxygen (Hildrew *et al.*, 2007) impacting ecosystem productivity, which was here measured through oxygen concentration changes. Body size is the primary target of global change, such as warming or harvesting (Daufresne *et al.*, 2009; Palkovacs *et al.*, 2018), and we show here that changes in the size structure of populations can have important ecological consequences.

In conclusion, we demonstrated that both intraspecific richness and the size structure of populations were important facet of biodiversity, inducing effects on prey community diversity and subsequently increase the rates of ecosystem processes. Ultimately, ecosystem services, such as carbon stocking, might be affected by intraspecific richness. These results add weigh to previous synthetic works (Chapter III, Koricheva & Hayes, 2018), reinforcing the call for considering changes of intraspecific diversity as an important ecological factor. Future investigations might aim at developing a general framework from genes to ecosystems to better understand the global links existing between biodiversity and ecosystem functioning, and ultimately ecosystem services.

Acknowledgements

We thank Kéoni Saint-Pe and Jérôme G. Prunier for their help for fish sampling. AR is financially supported by a Doctoral scholarship from the Université Fédérale de Toulouse. This work was undertaken at SETE, which is part of the “Laboratoire d’Excellence” (LABEX) entitled TULIP (ANR-10-LABX-41).

References

ALP, M., CUCHEROUSSET, J., BUORO, M. & LECERF, A. (2016) Phenological response of a key ecosystem function to biological invasion. *Ecology Letters* **19**, 519–527.

BATES, D., MAECHLER, M, BOLKER, B & WALKER, S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

BENJAMINI, Y. & HOCHBERG, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 13.

BROWN, J.H., GILLOOLY, J.F., ALLEN, A.P., SAVAGE, V.M. & WEST, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

CADOTTE, M.W., CARSCADDEN, K. & MIROTCHNICK, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48**, 1079–1087.

CAREAU, V. & GARLAND, T. (2012) Performance, Personality, and Energetics: Correlation, Causation, and Mechanism. *Physiological and Biochemical Zoology* **85**, 543–571.

CARLSON, B.E. & LANGKILDE, T. (2017) Body size variation in aquatic consumers causes pervasive community effects, independent of mean body size. *Ecology and Evolution* **7**, 9978–9990.

COLLIN, H. & FUMAGALLI, L. (2011) Evidence for morphological and adaptive genetic divergence between lake and stream habitats in European minnows (Phoxinus phoxinus, Cyprinidae). *Molecular Ecology* **20**, 4490–4502.

CRUTSINGER, G.M., COLLINS, M.D., FORDYCE, J.A., GOMPERT, Z., NICE, C.C. & SANDERS, N.J. (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* **313**, 966–968.

DAUFRESNE, M., LENGFELLNER, K. & SOMMER, U. (2009) Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences* **106**, 12788–12793.

DES ROCHES, S., POST, D.M., TURLEY, N.E., BAILEY, J.K., HENDRY, A.P., KINNISON, M.T., SCHWEITZER, J.A. & PALKOVACS, E.P. (2018) The ecological importance of intraspecific variation. *Nature Ecology & Evolution* **2**, 57–64.

DOWNING, A.L. & LEIBOLD, M.A. (2002) Ecosystem consequences of species richness and composition in pond food web. *Nature* **416**, 837-–841.

DUFFY, J.E. (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos* **99**, 201–219.

DUFFY, J.E., LEFCHECK, J.S., STUART-SMITH, R.D., NAVARRETE, S.A. & EDGAR, G.J. (2016) Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences* **113**, 6230–6235.

FOURTUNE, L., PRUNIER, J.G., MATHIEU-BEGNE, E., CANTO, N., VEYSSIERE, C., LOOT, G. & BLANCHET, S. (2018) Intraspecific genetic and phenotypic diversity: parallel processes and correlated patterns?

FRIDLEY, J.D. & GRIME, J.P. (2010) Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology* **91**, 2272–2283.

FROST, W.E. (1943) The natural history of the minnow, Phoxinus phoxinus. *The Journal of Animal Ecology* **12**, 139.

GESSNER, M.O., CHAUVET, E. & DOBSON, M. (1999) A perspective on leaf litter breakdown in streams. *Oikos* **85**, 377–384.

GESSNER, M.O., SWAN, C.M., DANG, C.K., MCKIE, B.G., BARDGETT, R.D., WALL, D.H. & HÄTTENSCHWILER, S. (2010) Diversity meets decomposition. *Trends in Ecology & Evolution* **25**, 372–380.

HARGRAVE, C.W., HAMBRIGHT, K.D. & WEIDER, L.J. (2011) Variation in resource consumption across a gradient of increasing intra- and interspecific richness. *Ecology* **92**, 1226–1235.

HILDREW, A.G., RAFFAELLI, D. & EDMONDS-BROWNS, R. (2007) *Body size: the structure and function of aquatic ecosystems*Cambridge University Press, Cambridge, UK.

HOOPER, D.U., CHAPIN, F.S., EWEL, J.J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J.H., LODGE, D.M., LOREAU, M., NAEEM, S., SCHMID, B., SETÄLÄ, H., SYMSTAD, A.J., VANDERMEER, J. & WARDLE, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.

HUGHES, A.R., INOUYE, B.D., JOHNSON, M.T.J., UNDERWOOD, N. & VELLEND, M. (2008) Ecological consequences of genetic diversity. *Ecology Letters* **11**, 609–623.

INGRAM, T., STUTZ, W.E. & BOLNICK, D.I. (2011) Does intraspecific size variation in a predator affect its diet diversity and top-down control of prey? *PLoS ONE* **6**, e20782.

JOHNSON, M.T.J., LAJEUNESSE, M.J. & AGRAWAL, A.A. (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* **9**, 24–34.

KEITH, P., PERSAT, H., FEUNTEUN, E. & ALLARDI, J. (2011) *Les poissons d'eau douce de France.*Muséum National d'Histoire Naturelle and Publications Biotope. Paris and Mèze.

KORICHEVA, J. & HAYES, D. (2018) The relative importance of plant intraspecific diversity in structuring arthropod communities: A meta-analysis. *Functional Ecology* **32**, 1704–1717.

LANDE, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* **76**, 5.

MCINTYRE, P.B., JONES, L.E., FLECKER, A.S. & VANNI, M.J. (2007) Fish extinctions alter nutrient recycling in tropical freshwaters. *Proceedings of the National Academy of Sciences* **104**, 4461–4466.

NAEEM, S., BUNKER, D.E., HECTOR, A., LOREAU, M. & PERRINGS, C. (2009) *Biodiversity, Ecosystem Functioning, and Human Wellbeing*. Oxford University Press.

PALKOVACS, E.P., KINNISON, M.T., CORREA, C., DALTON, C.M. & HENDRY, A.P. (2012) Fates beyond traits: ecological consequences of human-induced trait change: Fates beyond traits. *Evolutionary Applications* **5**, 183–191.

PALKOVACS, E.P., MORITSCH, M.M., CONTOLINI, G.M. & PELLETIER, F. (2018) Ecology of harvest-driven trait changes and implications for ecosystem management. *Frontiers in Ecology and the Environment* **16**, 20–28.

PARMESAN, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**, 637–669.

R CORE TEAM (2013) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

ROSENBLATT, A.E. & SCHMITZ, O.J. (2016) Climate change, nutrition, and bottom-up and top-down food web processes. *Trends in Ecology & Evolution*.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013a) Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology* **94**, 1046–1056.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013b) Population structure determines functional differences among species and ecosystem processes. *Nature Communications* **4**.

RUDOLF, V.H.W., RASMUSSEN, N.L., DIBBLE, C.J. & VAN ALLEN, B.G. (2014) Resolving the roles of body size and species identity in driving functional diversity. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20133203.

SCHMITZ, O.J., HAWLENA, D. & TRUSSELL, G.C. (2010) Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13**, 1199–1209.

SCHMITZ, O.J., RAYMOND, P.A., ESTES, J.A., KURZ, W.A., HOLTGRIEVE, G.W., RITCHIE, M.E., SCHINDLER, D.E., SPIVAK, A.C., WILSON, R.W., BRADFORD, M.A., CHRISTENSEN, V., DEEGAN, L., SMETACEK, V., VANNI, M.J. & WILMERS, C.C. (2014) Animating the carbon cycle. *Ecosystems* **17**, 344–359.

SIMPSON, E.H. (1949) Measurement of diversity. *Nature* **163**, 688.

TERBORGH, J. & ESTES, J.A. (2010) *Trophic cascades: predators, prey and the changing dynamics of nature.* Island Press, Washington DC.

VANNI, M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* **33**, 341–370.

WOODWARD, G., EBENMAN, B., EMMERSON, M., MONTOYA, J., OLESEN, J., VALIDO, A. & WARREN, P. (2005) Body size in ecological networks. *Trends in Ecology & Evolution* **20**, 402–409.

Supplementary information for Chapter VII.

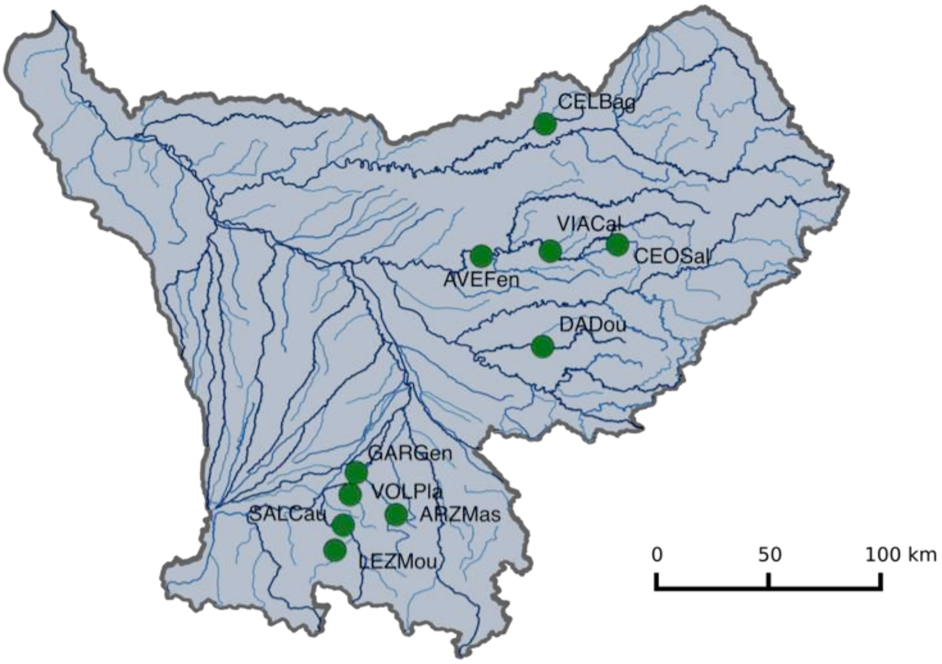

Figure VII.S1. Geographical distribution of the ten populations of European minnows (*Phoxinus phoxinus*) used in this study.

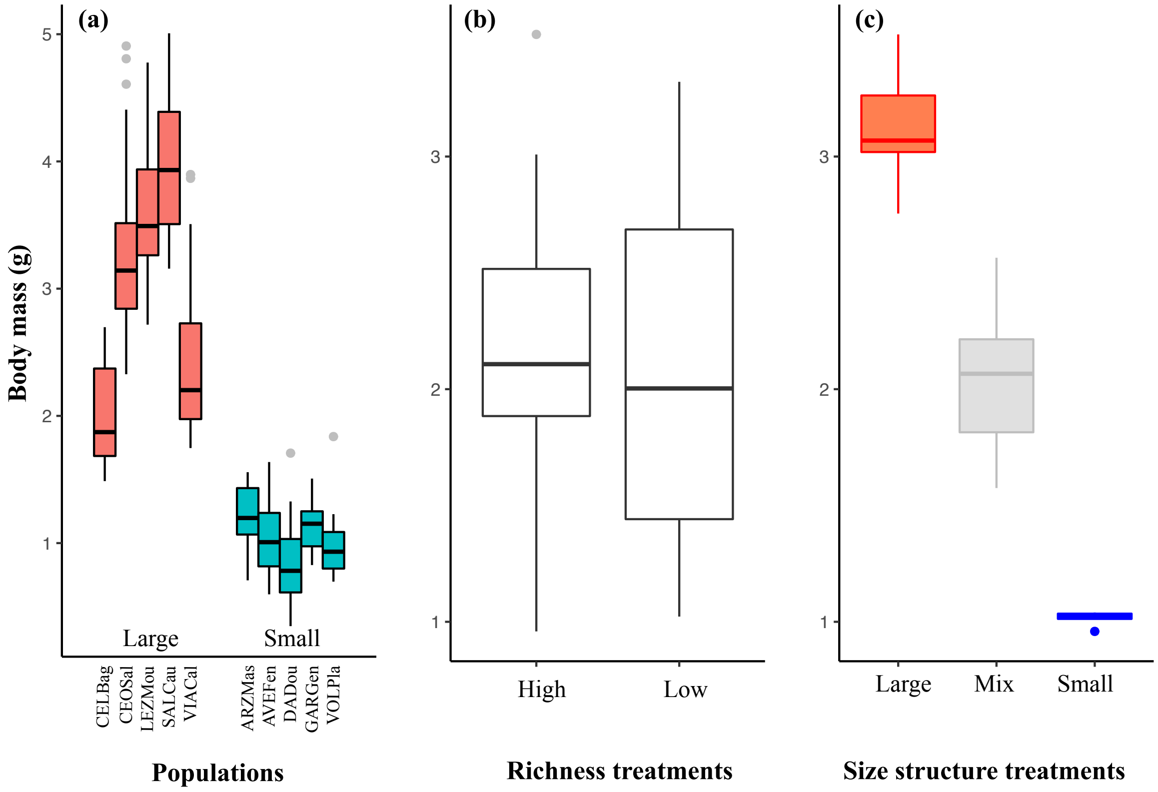

Figure VII.S2. Relationships between body mass of fish and **(a)** the population origin of fish, **(b)** the richness treatments (high = four populations, and low = two populations), and **(c)** the size structure treatments.

Table VII.S1. Six experimental treatments and the population origin of minnows (*Phoxinus phoxinus*) used in each of them.

Treatments					
Low richness Large individuals	Low richness Small individuals	Low richness L&S individuals	High richness Large individuals	High richness Small individuals	High richness - L&S individuals
CELBag-SALCau		CEOSal-VOLPla	CEOSal-VIASeg-CELBag-SALCau		CEOSal-CELBag-AVEfen-ARZMas
LEZMou-CEOSal		CELBag-GARGen	CEOSal-VIASeg-LEZMou-SALCau		CEOSal-VIASeg-AVEfen-VOLPla
VIACal-SALCau		VIASeg-ARZMas	CEOSal-VIASeg-LEZMou-CELbag		LEZMou-VIASeg-DADou-VOLPla
	GARGen-AVEFen	CEOSal-AVEFen		GARGen-AVEFen-DADou-ARZMas	CELBag-VIASeg-ARZMas-VOLPla
	VOLPla-ARZmas	LEZMou-DADou		VOLPla-AVEFen-DADou-ARZMas	LEZMou-SALCau-DADou-GARGen
	DADou-AVEFen	SALCau-AVEfen		VOLPla-AVEFen-DADou-GARGen	SALCau-CEOSal-GARGen-AVEFen

Chapitre VIII.

Discussion générale

Ce travail de thèse avait trois objectifs principaux qui visaient à identifier les déterminants et à quantifier les conséquences de la diversité intraspécifique. Tout d'abord, au travers d'une méta-analyse, nous avons testé l'importance écologique de la diversité intraspécifique de façon quantitative (Chapitre III). Brièvement, les résultats ont montré que (i) les effets écologiques de la *richesse* intraspécifique suivent une relation saturante et sont aussi élevés que ceux de la richesse interspécifique, et que (ii) les effets de la *variation* intraspécifique, quantifiés sur plus de 50 espèces, sont significatifs et sont plus élevés lorsque l'espèce ciblée est un producteur primaire plutôt qu'un consommateur, et plus forts sur les métriques écosystémiques que sur les communautés. Ensuite, nous avons quantifié la diversité intraspécifique des traits fonctionnels et des niches trophiques dans plusieurs populations sauvages de vairons afin d'en appréhender les déterminants. Les résultats suggèrent que les covariations entre les traits fonctionnels réponses et effets étaient importantes pour les dynamiques éco-évolutives. Ces covariations pouvaient varier entre populations à cause de mécanismes adaptatifs et non-adaptatifs (Chapitre IV). La variabilité trophique des vairons, mesurée à l'aide d'une analyse des isotopes stables, était liée à la morphologie des vairons mais contrainte par les conditions environnementales (Chapitre V). Enfin, nous avons étudié expérimentalement les effets écologiques de la diversité intraspécifique. La variation fonctionnelle entre populations a entraîné des différences écologiques (p.ex. abondance en zooplancton) entre mésocosmes aussi fortes qu'une augmentation de la température de l'eau de 2°C (Chapitre VI). Ces différences écologiques étaient assez fortes pour impacter la valeur sélective d'une génération suivante de vairons, générant alors une boucle de rétroaction éco-évolutive. Dans une dernière expérience, il a été montré que la richesse intraspécifique d'assemblages expérimentaux de populations de vairons entraînait une augmentation de la diversité de proies (invertébrées), et des processus écosystémiques (Chapitre VII).

VIII.1. Variabilité fonctionnelle et trophique

Les études observationnelles ont permis de caractériser des différences fonctionnelles et trophiques entre populations sauvages de vairons (Chapitres IV et V). Il était important de quantifier la variabilité fonctionnelle et trophique entre les populations de vairons étudiées et de comprendre leurs déterminants, car c'est au travers de ces deux facettes que les individus agissent sur les fonctions écologiques (Matthews *et al.*, 2011). Notamment, les mesures de traits fonctionnels et d'isotopes stables ont été réalisées au niveau individuel permettant de montrer que des contraintes intrinsèques aux organismes pouvaient lier la variabilité des traits entre eux et au régime alimentaire (Figure VIII.1). Ces mesures individuelles ont ensuite été transcrites au niveau des populations pour mettre en valeur des différences populationnelles sur plusieurs aspects (moyenne des traits, des niches trophiques, syndromes et lien entre niche fonctionnelle et trophique) et pour montrer que les conditions environnementales jouaient un rôle prépondérant pour modeler la variabilité des traits fonctionnels et de la niche trophique des vairons (Figure VIII.1). Cela confirme que la diversité intraspécifique est complexe à appréhender du fait de ses multiples déterminants.

Tout d'abord, nous avons mis en évidence que les populations de vairons étudiées étaient différentes fonctionnellement et trophiquement. Des études antérieures, menées lors de la thèse de Lisa Fourtune, ont montré que le niveau de différenciation morphologique entre populations était relativement faible (Pst = 0,30, Fourtune *et al.*, 2018) en comparaison avec d'autres espèces comme le goujon (*Gobio gobio*) (Pst = 0,65). La variabilité phénotypique mesurée dans les travaux de cette thèse - impliquant d'autres traits - était équivalente [taux métabolique (Pst = 0,35) et d'excrétion (Pst = 0,33)], ou plus forte dans le cas de la masse corporelle (Pst = 0,50). Cependant, ces niveaux de variabilité restent bien inférieurs à ceux observés chez le goujon. Malgré cette variabilité relativement faible, nous avons montré que les populations de vairons avaient des effets écosystémiques significatifs et potentiellement élevés (Chapitre VI). Cela peut s'expliquer par la variabilité trophique des populations qui, elle, était beaucoup plus élevée (p.ex. Pst = 0,83 pour la position trophique). Ces résultats suggèrent que les traits ne sont pas tous équivalents, et que le trait considéré est important pour pouvoir quantifier les effets écologiques à partir de la diversité fonctionnelle. De plus, il est possible que les effets de la diversité intraspécifique puissent être encore plus forts chez des espèces plus différenciées, renforçant l'idée que la diversité intraspécifique est un facteur écologique majeur.

Contraintes intrinsèques

Plusieurs mécanismes ont permis d'expliquer la variabilité des traits fonctionnels, dont les contraintes inhérentes aux individus engendrant des covariations entre traits (Armbruster *et al.*, 2014). Au niveau individuel un trait peut alors être contraint par d'autres traits et être impliqué dans de multiples covariations. En effet, un syndrome fonctionnel a été défini comme les corrélations entre plusieurs traits réponses et traits d'effets (Chapitre IV). Nous argumentons que ce syndrome fonctionnel place les traits fonctionnels au centre des dynamiques éco-évolutives (Matthews *et al.*, 2011) ; il lie les contraintes pesant sur les individus, générant de la variabilité sur les traits réponses (Torres-Dowdall *et al.*, 2012), aux effets écologiques des individus, via des corrélations avec les traits d'effets permettant aux organismes d'affecter le fonctionnement des écosystèmes (Lavorel & Garnier, 2002; Violle *et al.*, 2007, ANNEXE 1).

La variabilité fonctionnelle était aussi liée à la variabilité trophique entre populations (Chapitre V). Majoritairement étudiée au travers de la position trophique et de l'origine de la ressource consommée par les individus, la variabilité trophique était liée à la morphologie des individus (Skulason & Smith, 1995; Smith & Skulason, 1996). Aussi, des contraintes physiologiques peuvent définir le régime alimentaire des organismes. En effet, les populations avec de grands individus pouvaient avoir des positions trophiques plus faibles, ce qui est un résultat un peu contre-intuitif étant donné que les poissons les plus grands ont habituellement un position trophique élevée (Zanden *et al.*, 2000; Akin & Winemiller, 2008). Cela peut suggérer que les vairons les plus petits consommaient des ressources animales plus riches en protéines et en lipides pour soutenir un taux métabolique plus élevé (par unité de masse), alors que les vairons les plus gros consommaient une plus grande proportion de périphyton ou de débris végétaux. Cependant notre étude ne nous a pas permis de connaître précisément le régime alimentaire des populations de vairons. Pour aller plus loin dans l'étude de la niche trophique, des analyses complémentaires, telles que des contenus stomacaux, ou une meilleure caractérisation isotopique des invertébrés présents dans les rivières, seraient nécessaires. Cela permettrait de connaître plus précisément le type de ressource inclus dans le régime alimentaire des vairons (p.ex. la quantité relative d'invertébrés et de végétaux) (Araújo *et al.*, 2007; Zandonà *et al.*, 2017).

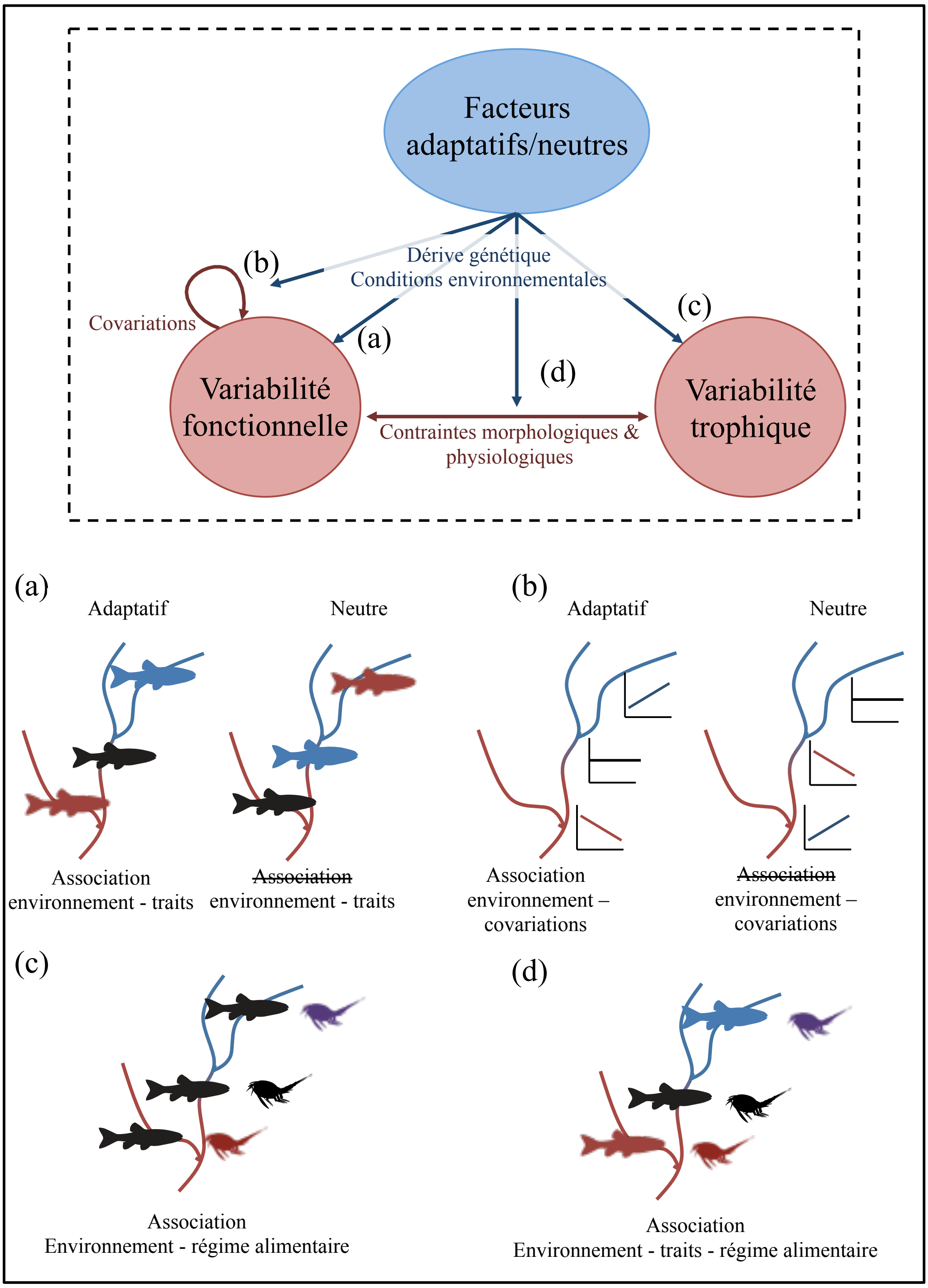

Figure VIII.1. Synthèse des résultats mis en évidence par les Chapitre IV et V montrant que les déterminants de la diversité intraspécifique sont multiples et complexes. En effet, il a été montré que des facteurs intrinsèques (flèches marrons) aux organismes pouvaient lier les traits les uns par rapport aux autres et à la variabilité trophique. Des facteurs externes (flèches bleues) ont pu modifier les traits **(a)** et le régime alimentaire **(c)** des organismes directement, ou en modifiant les liens intrinsèques aux individus **(b) (d)**. La couleur des poissons indique leur phénotype, la couleur de l'arrière-plan représente un réseau dendritique simplifié avec des facteurs environnementaux différents (p.ex. la température), et la couleur des icônes d'invertébrés représente des ressources différentes. La dérive génétique n'a été observée que pour les traits fonctionnels **(a)** et les covariations **(b)**. Elle n'est donc pas représentée pour la variabilité trophique **(c) (d).**

Rôle de l'environnement

En plus des covariations liant les traits et le régime alimentaire les uns avec les autres, l'environnement a joué un rôle important dans cette variabilité (Chapitre IV et V). Premièrement, la masse corporelle des vairons était dépendante des conditions environnementales (c.-à-d. interaction entre la température et la pression de prédation) vraisemblablement de façon adaptative (Figure VIII.1a, Chapitre IV). Ces résultats confirment que la masse corporelle est un trait central puisqu'elle influence à la fois les fonctions écologiques (Chapitre VI) et l'adaptation des individus à leur environnement. D'autres traits mesurés, tels que les taux métabolique et d'excrétion, variaient aussi de façon adaptative. Cependant, ils n'étaient ni liés à la température, ni à la prédation (deux paramètres étudiés dans le Chapitre IV) suggérant que d'autres paramètres environnementaux pourraient être impliqués. Deuxièmement, la variabilité trophique entre populations était également grandement dépendante de l'environnement (Figure VIII.1c, Chapitre V). Cet effet était attendu car les conditions environnementales des rivières peuvent déterminer les ressources disponibles pour les organismes, notamment les communautés d'invertébrés (Vannote *et al.*, 1980; Altermatt, 2013).

De plus, l'environnement a aussi affecté la covariation entre la masse corporelle et le métabolisme (Chapitre IV) montrant que les liens entre traits sont complexes et population-dépendants (Dingemanse *et al.*, 2007; Peiman & Robinson, 2017) (Figure VIII.1b). Etant donné que les traits sont contraints par l'environnement et que le régime alimentaire des organismes dépend en partie des traits, les relations entre les deux peuvent dépendre de l'environnement (Figure VIII.1d). En effet, l'environnement peut modifier la disponibilité des ressources et/ou induire des besoins nutritifs variables créant un décalage entre la morphologie et la niche trophique (Villéger *et al.*, 2017). Par exemple, une augmentation de la température peut induire une augmentation du métabolisme entraînant une augmentation en besoin en carbone pour soutenir une respiration plus élevée. Les organismes peuvent alors corriger leur régime alimentaire pour répondre à cette demande nutritive et optimiser leur valeur sélective (Boersma *et al.*, 2016; Rosenblatt & Schmitz, 2016). Il serait donc intéressant d'étudier de manière plus poussée le lien entre régime alimentaire et des traits autres que morpho-anatomiques, comme le taux métabolique, sous différentes conditions environnementales. Par exemple, des mesures expérimentales de taux métabolique et de régime alimentaire (p.ex. sur des ressources plus ou moins riches en carbone) pourraient être prises sous différentes températures, afin de tester si le métabolisme détermine le régime alimentaire et si cette relation est dépendante de l'environnement. Les liens décrits ci-dessus sont importants à prendre en compte car c'est en partie par des mécanismes trophiques que les organismes sont capables d'agir sur les communautés et les écosystèmes (Des Roches *et al.*, 2018).

Importance de l'influence relative de la sélection et de la plasticité

Pour aller plus loin dans la compréhension des causes de la diversité intraspécifique, il serait intéressant d'évaluer la contribution des facteurs évolutifs dans la variabilité des traits fonctionnels. Nous avons notamment effectué une analyse de génétique quantitative pour différencier la variabilité adaptative de la variabilité neutre sur certains traits, montrant que la dérive génétique pouvait engendrer des différences significatives entre populations de vairons (c.-à-d. différences comportementales et de covariations entre plusieurs traits, Chapitre IV, Figure VIII.1a, b). Cependant, il n'a pas pu être déterminé qui de la sélection ou de la plasticité était la base de la variabilité adaptative lorsqu'elle était présente. Des mesures de traits sur la descendance (F1 ou F2) des populations de vairons auraient permis de différencier la part héritable de la part plastique de la variabilité des traits fonctionnels (Leinonen *et al.*, 2013).

Par ailleurs, selon le trait considéré, les prévisions des actions relatives entre sélection et plasticité peuvent être différentes. En effet, les actions de la sélection et de la plasticité sont déterminées par l'héritabilité des traits et les liens entre traits et valeur sélective. Ainsi, la sélection naturelle pourrait agir plus fortement sur la variabilité des traits affectant fortement la survie et la reproduction (c.-à-d. valeur sélective). Par exemple, les traits d'histoire de vie ont beaucoup été étudiés car ils étaient considérés comme les traits immédiatement liés à la reproduction (Roff, 1992), ainsi que les traits comportementaux qui sont liés à la survie (Réale *et al.*, 2007). De nombreuses études sur l'adaptation locale ont déjà montré que plusieurs de ces traits étaient sous l'action de la sélection naturelle (Leinonen *et al.*, 2013). D'autres traits (qui peuvent pour la plupart être considérés comme des traits d'effets), comme la stoechiometrie corporelle ou le taux d'excrétion, dépendent des éléments présents dans l'environnement et affecteraient moins la valeur sélective. Alors, nous pourrions nous attendre à ce que ces traits varient plus du fait de la plasticité. Il a notamment été montré que la stoechiométrie en azote et en phosphore des épinoches (*Gasterosteus aculeatus*) dépendait plus fortement de l'environnement dans lequel les individus se développaient que des différences génétiques entre individus (Leal *et al.*, 2017). Peu d'études ont exploré les causes évolutives de ces traits, car ils ont été historiquement considérés comme peu pertinents pour la valeur sélective (voir Leal, Seehausen & Matthews, 2016 pour une perspective sur les traits stoechiométriques).

Dans un contexte où les changements globaux modifient constamment la variabilité des traits au sein des espèces (Parmesan, 2006; Darimont *et al.*, 2009), une connaissance plus précise de l'action relative des facteurs évolutifs et plastiques sur différents types de traits pourrait permettre d'inférer sur l'échelle de temps durant laquelle les changements peuvent se produire. En effet, les changements évolutifs se produisent généralement à une échelle de temps plus longue car ils nécessitent plusieurs générations. *A contrario*, par définition, les changements plastiques apparaîssent pendant la durée de vie d'un individu. Comme les traits d'effets affectent les processus écologiques, il serait pertinent d'évaluer la contribution des facteurs évolutifs et plastiques dans la variabilité de ces traits au niveau intraspécifique. En effet, cela permettrait d'améliorer les capacités de prédiction sur la rapidité avec laquelle les traits changent, et donc d'inférer sur le temps où les premières conséquences écologiques dues à ce changement de traits pourraient apparaître.

VIII.2. Relations biodiversité et fonctionnement des écosystèmes

Les autres chapitres de cette thèse avaient pour buts de comprendre les effets écologiques de la diversité intraspécifique (Chapitre III) et notamment des différences fonctionnelles et trophiques observées chez le vairon (Chapitre VI et VII). Les résultats ont suggéré que les conséquences d'un changement de la diversité intraspécifique sur la structure des communautés et le fonctionnement des écosystèmes pouvaient être considérables. En effet, chez les producteurs primaires une modification de la richesse intraspécifique affecte les fonctions écologiques aussi fortement qu'une modification de la richesse spécifique (Chapitre III). De plus, dans le Chapitre VI, il a été montré que les effets écologiques de la variation intraspécifique étaient aussi forts qu'une augmentation de la température de 2°C, et qu'elle devait alors être considérée comme un facteur écologique majeur.

Les résultats pris conjointement et confrontés à la littérature existante (voir notamment Whitham *et al.*, 2003, 2006) permettent de dresser une synthèse des relations entre la biodiversité et le fonctionnement des écosystèmes réunissant trois grands champs disciplinaires étudiant ces relations (Figure VIII.2). Ainsi, la diversité intraspécifique (populations), interspécifique (communautés) et les processus écosystémiques peuvent être étroitement liés et l'étude de cette relation tripartite est importante pour comprendre les cycles biogéochimiques dans l'environnement. Tout d'abord, les relations diversité interspécifique-fonctionnement des écosystèmes (sB-FE) ont fait émerger l'importance de la biodiversité pour les flux de matières et donc les processus écosystémiques (cf. Chapitre I) (Figure VIII.2). Notamment, les espèces ne sont pas toutes équivalentes fonctionnellement et selon les espèces présentent - leur nombre et leur abondance relative - dans une communauté, l'intensité des processus écosystémiques qui en résultent est différente (Hooper *et al.*, 2005; Cadotte, Carscadden, & Mirotchnick, 2011).

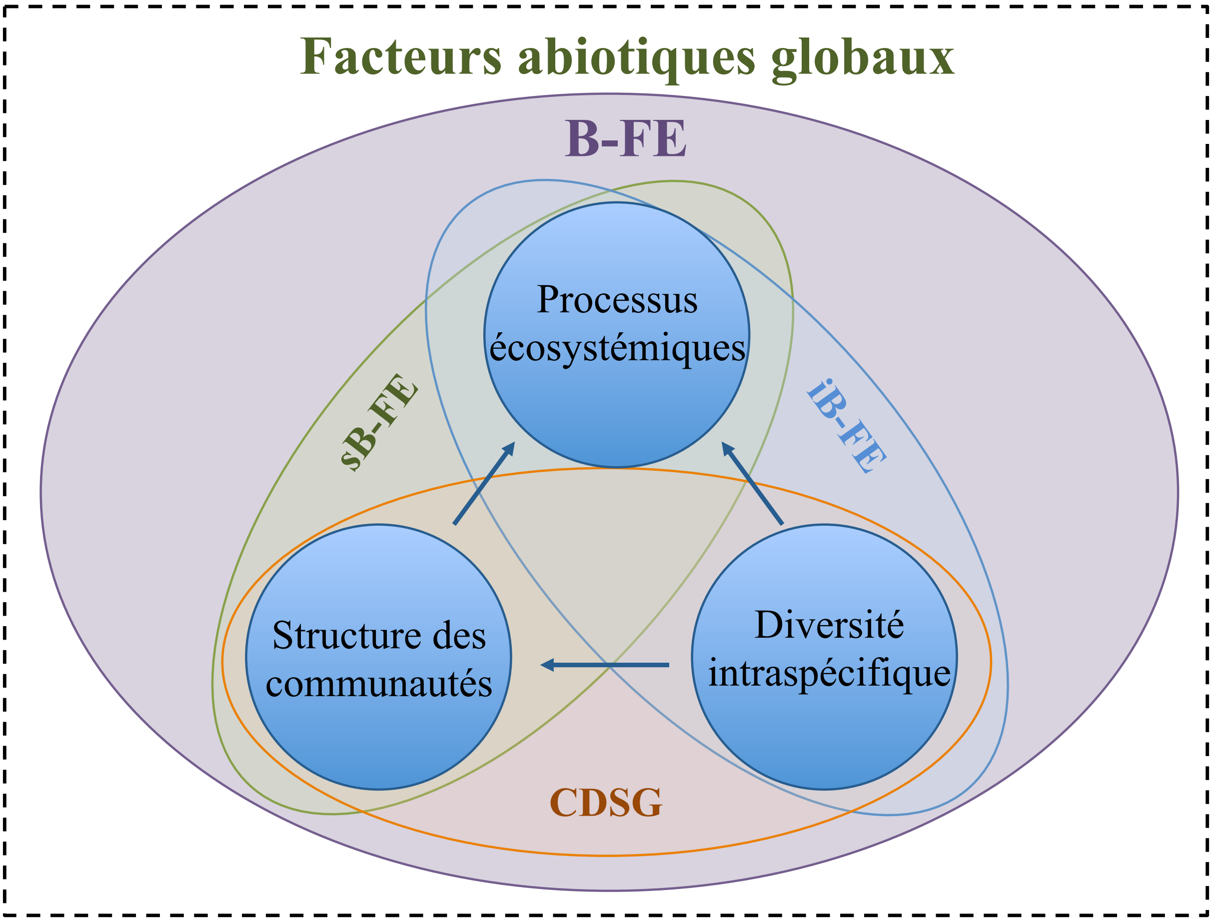

Figure VIII.2. Schéma conceptuel synthétisant les trois grands champs disciplinaires associés à l'étude du rôle écologique de la biodiversité et de ses effets sur le fonctionnement des écosystèmes (B-FE). Les iB-FE décrivent les relations entre biodiversité intraspécifique et fonctionnement des écosystèmes. Les CDSG décrivent les corrélations entre diversité spécifique et génétique. Bien que ces effets aient été décrits comme bilatéraux, nous avons montré des effets causaux de la diversité intraspécifique sur la structure des communautés. Enfin, les sB-FE ont historiquement décrit les relations entre biodiversité spécifique et fonctionnements des écosystèmes. Les chapitres III, VI et VII ont montré (i) des effets significatifs de la diversité (variation et richesse) intraspécifique sur plusieurs processus écosystémiques (iB-FE), (ii) des effets causaux sur la structure des communautés (CDSG), et (iii) des effets indirects de la diversité intraspécifique sur les processus écosystémiques en passant par un effet sur les communautés (CDSG puis sB-FE).

Relations entre diversité intraspécifique et structure des communautés

Les corrélations entre diversité spécifique et génétique (CDSG) ont historiquement fait émerger des relations entre la diversité génétique au niveau intraspécifique (*sensu* richesse intraspécifique) et la diversité spécifique au niveau des communautés (Vellend, 2003, 2005; Fourtune *et al.*, 2016) (Figure VIII.2). Ces liens peuvent notamment être causaux dans les cas où la diversité intraspécifique influence la diversité des espèces à une plus large échelle (le contraire a aussi été défini mais n'est pas discuté ici) (Vellend & Geber, 2005). Il a été suggéré que ces effets seraient dus, en autre, à la réduction du risque d'extinction et à la coexistence des espèces dans une communauté favorisée par des richesses génotypiques élevées (Vellend & Geber, 2005). En complément à ces travaux antérieurs, nos résultats suggèrent des effets causaux de la diversité intraspécifique sur la diversité spécifique d'échelons trophiques inférieurs, et montrent que la richesse intraspécifique chez une seule espèce peut affecter la structure de la communauté d'espèces environnantes (Chapitre III et VII).

Nous avons montré expérimentalement qu'une augmentation de la richesse intraspécifique chez le vairon pouvait entraîner une augmentation de la diversité de proies. Cet effet est probablement dû à des mécanismes trophiques ; quand la richesse est plus élevée, la richesse trophique pourrait aussi augmenter. Cela peut équilibrer les pressions sur les différents clades de proies et permettre une diversité plus élevée. Etant donné que les populations naturelles de vairons présentaient des richesses trophiques différentes (Chapitre V), cela suggère que des environnements hébergeant des populations avec différentes richesses pourraient présenter des communautés différentes (bien que les mécanismes sont probablement similaires, nous avons utilisé des mésocosmes lentiques, alors les inférences sur l'écologie des rivières sont à faire avec une extrême précaution). Cela montre également que la richesse intraspécifique chez les consommateurs peut induire des effets « top-down » sur les communautés, alors que les études précédentes rapportaient des résultats contrastés (Hargrave, Hambright, & Weider, 2011; Ingram, Stutz, & Bolnick, 2011; Carlson & Langkilde, 2017). Alors que ces études s'étaient principalement intéressées à la masse corporelle, nous avons constaté que la richesse sur d'autres traits que la masse corporelle pouvait être importante (Chapitre VII). Il a été vu précédemment que plusieurs traits pouvaient varier indépendamment de la masse corporelle dans les populations naturelles (p.ex. taux d'excrétion, comportement, et même niche trophique, Chapitre IV et V). Mesurer directement le régime alimentaire des individus dans les expériences, ou des traits potentiellement liés à l'acquisition de ressource [p.ex. la flexibilité du comportement alimentaire pourrait améliorer le partage des ressources entre individus (Dill, 1983)], pourrait apporter des indications additionnelles sur les mécanismes par lesquels la richesse intraspécifique affecte les communautés (Matthews *et al.*, 2011).

Enfin, les CDSG ont jusqu'à présent étudié principalement la richesse intraspécifique, mais plusieurs aspects de la diversité intraspécifique et des communautés peuvent interagir (Crutsinger *et al.*, 2008, 2014). Ces interactions concernent plusieurs métriques décrivant la structure des communautés, telles que l'abondance des individus ou la composition spécifique. Nous avons notamment montré que des variations fonctionnelles (c.-à-d. différence de masse corporelle) entre populations de vairons pouvaient engendrer des différences d'abondance des individus dans les communautés de zooplancton. Alors le cadre général des CDSG pourrait être étendues aux résultats décrivant les effets de la variation intraspécifique sur les communautés en générale (p.ex. Chapitre III et VI).

Relations entre diversité intraspécifique et fonctionnement des écosystèmes

En outre, les relations diversité intraspécifique-fonctionnement des écosystèmes (iB-FE) au sens large (c.-à-d. incluant variation et richesse intraspécifique) mettent en évidence que des différences phénotypiques entre populations (et même entre individus) peuvent affecter les processus écosystémiques (Whitham *et al.*, 2006; Bailey *et al.*, 2009) (Figure VIII.2). Ainsi, des environnements hébergeant des populations avec des différences de traits d'effets mènent à des écosystèmes fonctionnellement différents. Ces effets ont été décrits comme directs et indirects (Des Roches *et al.*, 2018, Chapitre III). Une grande partie des études relatent des effets directs, qui peuvent être trophiques (Chislock *et al.*, 2013) et non-trophiques (c.-à-d. via une modification du recyclage des nutriments, Evangelista *et al.*, 2017). Par exemple, certains de nos résultats montrent que la richesse intraspécifique peut entraîner une augmentation de la quantité d'azote dans le milieu (Chapitre VII). Cependant, il a aussi été proposé que les effets de la diversité intraspécifique puissent être indirects, c'est-à-dire qu'elle affecterait le fonctionnement des écosystèmes au travers des effets directs sur la structure des communautés (Chapitre III). Nos résultats tendent à confirmer ce postulat, puisque dans le Chapitre VII nous avons montré un effet de la richesse intraspécifique sur la structure des communautés d'invertébrés, puis cet effet était suivi d'un effet de la structure des communautés d'invertébrés sur le taux de décomposition de la matière organique.

Cependant, les études expérimentales se sont jusqu'à présent peu intéressées – explicitement - à ces effets indirects, malgré les répercussions importantes que cela peut avoir sur les processus écosystémiques. Les forces relatives des effets directs et indirects devraient dépendre du type de trait et de l'organisme considéré. En effet, certains organismes sont fortement liés à un processus écosystémique (p.ex. les décomposeurs), alors leurs effets devraient être principalement directs. D'autres organismes (p.ex. les prédateurs), plus haut dans la chaîne trophique, devraient induire principalement des effets indirects par leurs effets sur les communautés car ils ne sont pas directement liés à un processus écosystémique. De plus, certains traits pourraient être plus fortement liés à l'écosystème qu'aux communautés (p.ex. stoechiométrie), et *vice-versa* (p.ex. morphologie trophique). Ainsi certains traits seraient importants pour les prédictions des effets directs de la diversité intraspécifique alors que d'autres permettraient d'inférer sur des effets indirects via les communautés.

Rôle médiateur de l'environnement

Enfin, les populations, les communautés et les écosystèmes sont tous trois dépendants des contraintes imposées les facteurs environnementaux globaux (p.ex. la température) (Parmesan, 2006; Stomp *et al.*, 2011; Yvon-Durocher *et al.*, 2015). Comme ces trois niveaux d'organisation biologique sont liés les uns aux autres, l'effet de l'environnement sur l'un d'eux peut se répercuter sur les autres. L'environnement joue alors le rôle de médiateur entre la diversité intraspécifique, les communautés et les processus écosystémiques. Aussi, l'environnement pourrait ajouter un niveau de complexité en générant des effets écologiques contexte-dépendants. Autrement dit, selon les conditions environnementales, les effets écologiques de la diversité intraspécifique pourraient être différents du fait de l'effet de l'environnement sur les communautés et les écosystèmes, mais aussi car les individus supporteraient des contraintes différentes pouvant modifier leurs traits et donc *in fine* leurs effets écologiques. Curieusement, cette contexte-dépendance n'est pas consistante puisque le peu de travaux qui l'ont étudiée (faisant varier la température, l'intensité lumineuse ou encore la concentration en nutriment) ont montré des résultats contrastés (Chapitre VI, Burkle *et al.*, 2013; El-Sabaawi *et al.*, 2015; Fryxell & Palkovacs, 2017). Ces expériences ont probablement eu lieu sur des temps trop courts (c.-à-d. inférieurs à une génération de l'espèce ciblée) pour que les traits des individus soient impactés. Des expériences plus longues pourraient permettre la mise en place de plusieurs générations au cours desquelles une adaptation des individus (et même des fonctions écologiques) aux variations environnementales pourrait apparaître, entraînant une contexte-dépendance des effets écologiques de la diversité intraspécifique.

Actuellement les changements globaux s'additionnent aux variations environnementales naturelles pour modeler la biodiversité. Plusieurs types de pressions anthropiques affectent la diversité intraspécifique, tels que le changement climatique, l'introduction d'espèces invasives, la perte d'habitats ou encore le prélèvement d'individus (Parmesan, 2006; Darimont *et al.*, 2009). Ces modifications à l'échelle intraspécifique peuvent donc se répercuter sur la structure des communautés et le fonctionnement des écosystèmes (Mimura *et al.*, 2016). Bien que ces conséquences écologiques soient potentiellement fortes (Chapitre III et VI), les effets indirects des modifications de la diversité intraspécifique - du fait d'impacts anthropiques - sur les communautés et les écosystèmes restent très peu explorés. Quelques nouveaux travaux conceptuels ont récemment émergé, mettant en exergue les potentiels effets écosystémiques d'un changement diversité intraspécifique (Mimura *et al.*, 2016; Palkovacs *et al.*, 2018; Závorka *et al.*, 2018). Cependant, beaucoup reste à faire puisque ces travaux sont encore marginaux. Il y a un réel besoin de nouvelles études fondamentales afin de prédire avec plus de précisions les effets écologiques d'un changement de la diversité intraspécifique. Ces études fondamentales permettront de construire une base solide sur laquelle des études plus appliquées pourront s'appuyer notamment pour mettre en place des plans de gestions de la diversité intraspécifique efficaces.

VIII.3. Vers une quantification plus réaliste du rôle écologique de la diversité intraspécifique

Les travaux de cette thèse ont permis de mettre en évidence le rôle de la diversité intraspécifique dans les écosystèmes. Cependant, des études sont encore nécessaires afin d'évaluer de manière plus réaliste de l'importance écologique la diversité intraspécifique. Alors, l'une des étapes clés sera de complexifier les designs expérimentaux, afin de refléter un peu plus ce qu'il se passe en milieu naturel, et de confirmer que les effets de la diversité intraspécifique ne sont pas qu'un bruit dans des systèmes complexes.

Quelques études ont déjà fait varier des facteurs abiotiques, montrant que les effets de la diversité intraspécifique pouvaient résister à un certain niveau de bruit environnemental (p.ex. Chapitre VI, Burkle *et al.*, 2013; El-Sabaawi *et al.*, 2015). Néanmoins, la diversité intraspécifique a souvent été manipulée chez une seule espèce à la fois. Comme en atteste la méta-analyse (Chapitre III), peu d'études ont manipulé la diversité intraspécifique chez plusieurs espèces (voir Booth & Grime, 2003; Fridley & Grime, 2010). Cependant, en milieu naturel, les espèces interagissent entre elles, notamment par le biais de la compétition. Donc, les espèces accompagnatrices de l'espèce ciblée ont potentiellement un rôle important à jouer dans la quantification des effets écologiques de la diversité intraspécifique. En effet, les espèces sympatriques ont potentiellement co-évolué (si l'on omet les espèces envahissantes), et présentent probablement des niches écologiques complémentaires. Inclure des espèces compétitrices dans les expériences pourrait masquer les effets de la diversité intraspécifique car toutes les niches écologiques seraient occupées, minimisant l'expression de la diversité intraspécifique. Alternativement, le fait que les espèces aient co-évolué pourrait engendrer des effets plus forts, car les différences de niches occupées par des populations différentes pourraient être exacerbées en présence des autres espèces. Alors les prochaines études devraient inclure des espèces compétitrices dans les expériences, et même manipuler la diversité intraspécifique chez plusieurs espèces à la fois, pour mieux refléter la réalité. Cela permettrait également un meilleur partitionnement de l'importance relative de la diversité intraspécifique chez plusieurs espèces interagissant entre elles.

Enfin, les conséquences de la diversité intraspécifique ont majoritairement été étudiées au travers des effets directs des individus sur la structure des communautés et le fonctionnement des écosystèmes. Cependant, les effets indirects restent encore à explorer, puisque la diversité intraspécifique pourrait affecter indirectement les communautés et les écosystèmes via une modification de la dynamique des populations (Hendry, 2016). En effet, des individus ayant une descendance plus ou moins nombreuse peuvent moduler la taille de la population. Cette différence d'abondance se répercuterait alors sur la structure des communautés et le fonctionnement des écosystèmes (p.ex. Best *et al.*, 2017). Ainsi, même en présentant des traits d'effets similaires, des individus pourraient avoir des effets écologiques différents selon leur succès reproducteur. Une prochaine étape sera de différencier les forces relatives et les interactions entre les effets directs et indirects via une modification de la dynamique de population. Par exemple, une augmentation de la densité de population pourrait altérer les effets directs en les inhibant ou en les amplifiant. Afin d'essayer de démêler ces effets, des expériences incluant plusieurs temps de générations pourraient être conduites. Cela permettrait de quantifier les effets directs à court terme puis les effets indirects à plus long terme grâce à un suivi temporel des dynamiques des communautés et des écosystèmes.

VIII.4. Conclusion

Pour conclure, nous avons utilisé des approches méta-analytique, observationnelle et expérimentale qui ont permis de montrer que la diversité intraspécifique était complexe à appréhender et jouait un rôle essentiel pour le fonctionnement des écosystèmes. Une étude méta-analytique a d'abord permis de montrer, sur près de 90 études et 64 espèces, que les effets écologiques de la diversité intraspécifique étaient forts. Ensuite, nous avons mis en évidence des différences fonctionnelles et trophiques entre populations sauvages de vairons. Cette diversité était déterminée par les conditions environnementales, des processus évolutifs et les covariations entre les traits. Enfin, des expériences ont montré que ces variations fonctionnelles, ainsi que la richesse génétique des populations, pouvaient avoir des conséquences sur la structure des communautés et le fonctionnement des écosystèmes. Bien que ces travaux de thèse contribuent à généraliser l'idée que la diversité intraspécifique est essentielle pour la structure des communautés et le fonctionnement des écosystèmes, plusieurs perspectives restent à explorer. L'un des enjeux essentiels sera notamment de comprendre comment les organismes s'adaptent face aux changements globaux, et de prédire les effets écologiques de ces adaptations.

Références bibliographiques

ABBOTT, J.M., GROSBERG, R.K., WILLIAMS, S.L. & STACHOWICZ, J.J. (2017) Multiple dimensions of intraspecific diversity affect biomass of eelgrass and its associated community. *Ecology* **98**, 3152–3164.

AKIN, S. & WINEMILLER, K.O. (2008) Body size and trophic position in a temperate estuarine food web. *Acta Oecologica* **33**, 144–153.

ALP, M., CUCHEROUSSET, J., BUORO, M. & LECERF, A. (2016) Phenological response of a key ecosystem function to biological invasion. *Ecology Letters* **19**, 519–527.

ALP, M., KELLER, I., WESTRAM, A.M. & ROBINSON, C.T. (2012) How river structure and biological traits influence gene flow: a population genetic study of two stream invertebrates with differing dispersal abilities: Biological traits and gene flow in stream invertebrates. *Freshwater Biology* **57**, 969–981.

ALTERMATT, F. (2013) Diversity in riverine metacommunities: a network perspective. *Aquatic Ecology* **47**, 365–377.

ARAÚJO, M.S., BOLNICK, D.I., MACHADO, G., GIARETTA, A.A. & DOS REIS, S.F. (2007) Using δ13C stable isotopes to quantify individual-level diet variation. *Oecologia* **152**, 643–654.

ARMBRUSTER, W.S., PELABON, C., BOLSTAD, G.H. & HANSEN, T.F. (2014) Integrated phenotypes: understanding trait covariation in plants and animals. *Philosophical Transactions of the Royal Society B: Biological Sciences* **369**, 20130245–20130245.

BAILEY, J.K., SCHWEITZER, J.A., UBEDA, F., KORICHEVA, J., LEROY, C.J., MADRITCH, M.D., REHILL, B.J., BANGERT, R.K., FISCHER, D.G., ALLAN, G.J. & WHITHAM, T.G. (2009) From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1607–1616.

BARBOUR, R.C., O'REILLY-WAPSTRA, J.M., DE LITTLE, D.W., JORDAN, G.J., STEANE, D.A., HUMPHREYS, J.R., BAILEY, J.K., WHITHAM, T.G. & POTTS, B.M. (2009) A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology* **90**, 1762–1772.

BARDGETT, R.D. & WARDLE, D.A. (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* **84**, 2258–2268.

BARTELS, P., CUCHEROUSSET, J., STEGER, K., EKLÖV, P., TRANVIK, L.J. & HILLEBRAND, H. (2012) Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* **93**, 1173–1182.

BASSAR, R.D., FERRIERE, R., LÓPEZ-SEPULCRE, A., MARSHALL, M.C., TRAVIS, J., PRINGLE, C.M. & REZNICK, D.N. (2012) Direct and indirect ecosystem effects of evolutionary adaptation in the Trinidadian guppy (*Poecilia reticulata*). *The American Naturalist* **180**, 167–185.

BASSAR, R.D., MARSHALL, M.C., LOPEZ-SEPULCRE, A., ZANDONA, E., AUER, S.K., TRAVIS, J., PRINGLE, C.M., FLECKER, A.S., THOMAS, S.A., FRASER, D.F. & REZNICK, D.N. (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences* **107**, 3616–3621.

BEAMISH, R.J. & BOUILLON, D.R. (1993) Pacific salmon production trends in relation to climate. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1002–1016.

BEST, R.J., ANAYA-ROJAS, J.M., LEAL, M.C., SCHMID, D.W., SEEHAUSEN, O. & MATTHEWS, B. (2017) Transgenerational selection driven by divergent ecological impacts of hybridizing lineages. *Nature Ecology & Evolution* **1**, 1757–1765.

BESTION, E., CUCHEROUSSET, J., TEYSSIER, A. & COTE, J. (2015) Non-consumptive effects of a top-predator decrease the strength of the trophic cascade in a four-level terrestrial food web. *Oikos* **124**, 1597–1602.

BIRO, P.A., BECKMANN, C. & STAMPS, J.A. (2010) Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences* **277**, 71–77.

BIRO, P.A. & DINGEMANSE, N.J. (2009) Sampling bias resulting from animal personality. *Trends in Ecology & Evolution* **24**, 63–66.

BLANQUART, F., KALTZ, O., NUISMER, S.L. & GANDON, S. (2013) A practical guide to measuring local adaptation. *Ecology Letters* **16**, 1195–1205.

BOERSMA, M., MATHEW, K.A., NIEHOFF, B., SCHOO, K.L., FRANCO-SANTOS, R.M. & MEUNIER, C.L. (2016) Temperature driven changes in the diet preference of omnivorous copepods: no more meat when it's hot? *Ecology Letters* **19**, 45–53.

BOLNICK, D.I., SVANBÄCK, R., FORDYCE, J.A., YANG, L.H., DAVIS, J.M., HULSEY, C.D. & FORISTER, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**, 1–28.

BOOTH, R.E. & GRIME, J.P. (2003) Effects of genetic impoverishment on plant community diversity. *Journal of Ecology* **91**, 721–730.

BROWN, J.H., GILLOOLY, J.F., ALLEN, A.P., SAVAGE, V.M. & WEST, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

BRUNNER, F.S., ANAYA-ROJAS, J.M., MATTHEWS, B. & EIZAGUIRRE, C. (2017) Experimental evidence that parasites drive eco-evolutionary feedbacks. *Proceedings of the National Academy of Sciences* **114**, 3678–3683.

BURKLE, L.A., SOUZA, L., GENUNG, M.A. & CRUTSINGER, G.M. (2013) Plant genotype, nutrients, and G X E interactions structure floral visitor communities. *Ecosphere* **4**.

BURTON, T., KILLEN, S.S., ARMSTRONG, J.D. & METCALFE, N.B. (2011) What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B: Biological Sciences* **278**, 3465–3473.

CADOTTE, M.W., CARSCADDEN, K. & MIROTCHNICK, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48**, 1079–1087.

CARDINALE, B.J. (2011) Biodiversity improves water quality through niche partitioning. *Nature* **472**, 86–89.

CARDINALE, B.J., DUFFY, J.E., GONZALEZ, A., HOOPER, D.U., PERRINGS, C., VENAIL, P., NARWANI, A., MACE, G.M., TILMAN, D., WARDLE, D.A., KINZIG, A.P., DAILY, G.C., LOREAU, M., GRACE, J.B., LARIGAUDERIE, A., ET AL. (2012) Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67.

CARDINALE, B.J., PALMER, M.. & COLLINS, S.. (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**, 426–429.

CAREAU, V., THOMAS, D., HUMPHRIES, M.M. & RÉALE, D. (2008) Energy metabolism and animal personality. *Oikos* **117**, 641–653.

CARLSON, B.E. & LANGKILDE, T. (2017) Body size variation in aquatic consumers causes pervasive community effects, independent of mean body size. *Ecology and Evolution* **7**, 9978–9990.

CHASE, J.M. (2000) Are there real differences among aquatic and terrestrial food webs? *Trends in Ecology & Evolution* **15**, 408–412.

CHISLOCK, M.F., SARNELLE, O., OLSEN, B.K., DOSTER, E. & WILSON, A.E. (2013) Large effects of consumer offense on ecosystem structure and function. *Ecology* **94**, 2375–2380.

CLARKE, A., MAC NALLY, R., BOND, N. & LAKE, P.S. (2008) Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology* **53**, 1707–1721.

CLOBERT, J., LE GALLIARD, J.-F., COTE, J., MEYLAN, S. & MASSOT, M. (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* **12**, 197–209.

COLLIN, H. & FUMAGALLI, L. (2011) Evidence for morphological and adaptive genetic divergence between lake and stream habitats in European minnows (*Phoxinus phoxinus*, Cyprinidae). *Molecular Ecology* **20**, 4490–4502.

COLLIN, H. & FUMAGALLI, L. (2015) The role of geography and ecology in shaping repeated patterns of morphological and genetic differentiation between European minnows (*Phoxinus phoxinus*) from the Pyrenees and the Alps. *Biological Journal of the Linnean Society* **116**, 691–703.

CORNELISSEN, J.H.C., LAVOREL, S., GARNIER, E., DÍAZ, S., BUCHMANN, N., GURVICH, D.E., REICH, P.B., STEEGE, H. TER, MORGAN, H.D., HEIJDEN, M.G.A. VAN DER, PAUSAS, J.G. & POORTER, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335.

COVICH, A.P., AUSTEN, M.C., BÄRLOCHER, F., CHAUVET, E., CARDINALE, B.J., BILES, C.L., INCHAUSTI, P., DANGLES, O., SOLAN, M., GESSNER, M.O., STATZNER, B. & MOSS, B. (2004a) The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. *BioScience* **54**, 767–775.

COVICH, A.P., EWEL, K.C., HALL, R., O., GILLER, P.S., GOEDKOOP, W. & MERRITT, D.M. (2004b) Ecosystem services provided by freshwater benthos. In *Sustaining biodiversity and ecosystem services in soils and sediments* Island Press, Washington DC.

CRAWFORD, K.M. & RUDGERS, J.A. (2013) Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology* **94**, 1025–1035.

CRUTSINGER, G.M., REYNOLDS, W.N., CLASSEN, A.T. & SANDERS, N.J. (2008) Disparate effects of plant genotypic diversity on foliage and litter arthropod communities. *Oecologia* **158**, 65–75.

CRUTSINGER, G.M., RODRIGUEZ-CABAL, M.A., RODDY, A.B., PEAY, K.G., BASTOW, J.L., KIDDER, A.G., DAWSON, T.E., FINE, P.V.A. & RUDGERS, J.A. (2014a) Genetic variation within a dominant shrub structures green and brown community assemblages. *Ecology* **95**, 387–398.

CRUTSINGER, G.M., RUDMAN, S.M., RODRIGUEZ-CABAL, M.A., MCKOWN, A.D., SATO, T., MACDONALD, A.M., HEAVYSIDE, J., GERALDES, A., HART, E.M., LEROY, C.J. & EL-SABAAWI, R.W. (2014b) Testing a 'genes-to-ecosystems' approach to understanding aquatic-terrestrial linkages. *Molecular Ecology* **23**, 5888–5903.

CRUTSINGER, G.M., SANDERS, N.J. & CLASSEN, A.T. (2009) Comparing intra- and inter-specific effects on litter decomposition in an old-field ecosystem. *Basic and Applied Ecology* **10**, 535–543.

CUCHEROUSSET, J., AYMES, J.C., SANTOUL, F. & CÉRÉGHINO, R. (2007) Stable isotope evidence of trophic interactions between introduced brook trout *Salvelinus fontinalis* and native brown trout *Salmo trutta* in a mountain stream of south-west France. *Journal of Fish Biology* **71**, 210–223.

CUCHEROUSSET, J. & OLDEN, J.D. (2011) Ecological impacts of nonnative freshwater fishes. *Fisheries* **36**, 215–230.

DARIMONT, C.T., CARLSON, S.M., KINNISON, M.T., PAQUET, P.C., REIMCHEN, T.E. & WILMERS, C.C. (2009) Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences* **106**, 952–954.

DARWIN, C. (1859) *On the origin of species by natural selection, or the preservation of favoured races in the struggle for life*. London John Murray.

DAUFRESNE, M., LENGFELLNER, K. & SOMMER, U. (2009) Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences* **106**, 12788–12793.

DAY, T. & MCPHAIL, J.D. (1996) The effect of behavioural and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosteus sp.*). *Oecologia* **108**, 380–388.

De Meester, L. (1996) Evolutionary potential and local genetic differentiation in a phenotypically plastic trait of a cyclical parthenogen, *Daphnia magna*. *Evolution* **50**, 1293–1298.

Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T., Schweitzer, J.A. & Palkovacs, E.P. (2018) The ecological importance of intraspecific variation. *Nature Ecology & Evolution* **2**, 57–64.

Des Roches, S., Shurin, J.B., Schluter, D. & Harmon, L.J. (2013) Ecological and evolutionary effects of stickleback on community structure. *PLoS ONE* **8**, e59644.

DeWitt, T.J., Sih, A. & Wilson, D.S. (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution* **13**, 77–81.

Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P. & Pearse, W.D. (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3**, 2958–2975.

Dill, L.M. (1983) Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 398–408.

Dingemanse, N.J., Wright, J., Kazem, A.J.N., Thomas, D.K., Hickling, R. & Dawnay, N. (2007) Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology* **76**, 1128–1138.

Downing, A.L. & Leibold, M.A. (2002) Ecosystem consequences of species richness and composition in pond food web. *Nature* **416**, 837-–841.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**, 163.

Duffy, J.E., Godwin, C.M. & Cardinale, B.J. (2017) Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* **549**, 261–264.

Duffy, J.E., Lefcheck, J.S., Stuart-Smith, R.D., Navarrete, S.A. & Edgar, G.J. (2016) Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences* **113**, 6230–6235.

Eckert, C.G., Samis, K.E. & Lougheed, S.C. (2008) Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. *Molecular Ecology* **17**, 1170–1188.

El-Sabaawi, R.W., Bassar, R.D., Rakowski, C., Marshall, M.C., Bryan, B.L., Thomas, S.N., Pringle, C., Reznick, D.N. & Flecker, A.S. (2015) Intraspecific phenotypic differences in fish affect ecosystem processes as much as bottom-up factors. *Oikos* **124**, 1181–1191.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H. & Sterner, R.W. (2000) Nutritional constraints in terrestrial and freshwater food webs **408**, 3.

Endler, J.A. (1986) *Natural selection in the wild*. Princeton University Press.

Evangelista, C., Lecerf, A., Britton, J.R. & Cucherousset, J. (2017) Resource composition mediates the effects of intraspecific variability in nutrient recycling on ecosystem processes. *Oikos* **126**, 1439–1450.

Fourtune, L., Paz-Vinas, I., Loot, G., Prunier, J.G. & Blanchet, S. (2016) Lessons from the fish: a multi-species analysis reveals common processes underlying similar species-genetic diversity correlations. *Freshwater Biology* **61**, 1830–1845.

Fourtune, L., Prunier, J.G., Mathieu-Begne, E., Canto, N., Veyssiere, C., Loot, G. & Blanchet, S. (2018) Intraspecific genetic and phenotypic diversity: parallel processes and correlated patterns?

FREYHOF, J. & KOTTELAT, M. (2008) Phoxinus phoxinus: the IUCN red list of threatened species. International Union for Conservation of Nature. Http://www.iucnredlist.org/details/17067/0 [accessed 22 September 2018].

FRIDLEY, J.D. & GRIME, J.P. (2010) Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology* **91**, 2272–2283.

FROST, W.E. (1943) The natural history of the minnow, *Phoxinus phoxinus*. *The Journal of Animal Ecology* **12**, 139.

FRYXELL, D.C. & PALKOVACS, E.P. (2017) Warming strengthens the ecological role of intraspecific variation in a predator. *Copeia* **105**, 523–532.

FUSSMANN, G.F., LOREAU, M. & ABRAMS, P.A. (2007) Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology* **21**, 465–477.

GACIA, E., BUCHACA, T., BERNAL-MENDOZA, N., SABÁS, I., BALLESTEROS, E. & VENTURA, M. (2018) Non-native minnows threaten quillwort populations in high mountain shallow lakes. *Frontiers in Plant Science* **9**.

GAGIC, V., BARTOMEUS, I., JONSSON, T., TAYLOR, A., WINQVIST, C., FISCHER, C., SLADE, E.M., STEFFAN-DEWENTER, I., EMMERSON, M., POTTS, S.G., TSCHARNTKE, T., WEISSER, W. & BOMMARCO, R. (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20142620–20142620.

GARNIER, E., CORTEZ, J., BILLÈS, G., NAVAS, M.-L., ROUMET, C., DEBUSSCHE, M., LAURENT, G., BLANCHARD, A., AUBRY, D., BELLMANN, A., NEILL, C. & TOUSSAINT, J.-P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**, 2630–2637.

GASTON, K.J. (1996) *Biodiversity. A biology of numbers and differences*. Blackwell, Oxford, U.K.

GESSNER, M.O., CHAUVET, E. & DOBSON, M. (1999) A perspective on leaf litter breakdown in streams. *Oikos* **85**, 377–384.

GILLOOLY, J.F. (2001) Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251.

GRANT, C.E.H., LOWE, W.H. & FAGAN, W.F. (2007) Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* **10**, 165–175.

HARGRAVE, C.W., HAMBRIGHT, K.D. & WEIDER, L.J. (2011) Variation in resource consumption across a gradient of increasing intra- and interspecific richness. *Ecology* **92**, 1226–1235.

HARMON, L.J., MATTHEWS, B., DES ROCHES, S., CHASE, J.M., SHURIN, J.B. & SCHLUTER, D. (2009) Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* **458**, 1167–1170.

HARTL, D.L. & CLARK, A.G. (1997) *Principles of population genetics*. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

HAWLENA, D. & SCHMITZ, O.J. (2010) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *The American Naturalist* **176**, 537–556.

HAWLENA, D., STRICKLAND, M.S., BRADFORD, M.A. & SCHMITZ, O.J. (2012) Fear of predation slows plant-Litter decomposition. *Science* **336**, 1434–1438.

HENDRY, A.P. (2016) *Eco-evolutionary dynamics.* Princeton University Press.

HILDREW, A.G., RAFFAELLI, D. & EDMONDS-BROWNS, R. (2007) *Body size: the structure and function of aquatic ecosystems.* Cambridge University Press, Cambridge, UK.

HOFFMANN, A.A. & MERILÄ, J. (1999) Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology & Evolution* **14**, 96–101.

HOFFMANN, A.A. & WILLI, Y. (2008) Detecting genetic responses to environmental change. *Nature Reviews Genetics* **9**, 421–432.

HOLDICH, D.M. (1993) A review of astaciculture: freshwater crayfish farming. *Aquatic Living Resources* **6**, 307–317.

HOOPER, D.U., ADAIR, E.C., CARDINALE, B.J., BYRNES, J.E.K., HUNGATE, B.A., MATULICH, K.L., GONZALEZ, A., DUFFY, J.E., GAMFELDT, L. & O'CONNOR, M.I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*.

HOOPER, D.U., CHAPIN, F.S., EWEL, J.J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J.H., LODGE, D.M., LOREAU, M., NAEEM, S., SCHMID, B., SETÄLÄ, H., SYMSTAD, A.J., VANDERMEER, J. & WARDLE, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.

HOWETH, J.G., WEIS, J.J., BRODERSEN, J., HATTON, E.C. & POST, D.M. (2013) Intraspecific phenotypic variation in a fish predator affects multitrophic lake metacommunity structure. *Ecology and Evolution* **3**, 5031–5044.

HUGHES, A.R., INOUYE, B.D., JOHNSON, M.T.J., UNDERWOOD, N. & VELLEND, M. (2008) Ecological consequences of genetic diversity. *Ecology Letters* **11**, 609–623.

HUTCHINGS, M.J. & DE KROON, H. (1994) Foraging in plants: the role of morphological plasticity in resource acquisition. In *Advances in Ecological Research*. Elsevier.

IMRE, I., MCLAUGHLIN, R.L. & NOAKES, D.L.G. (2002) Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. *Journal of Fish Biology* **61**, 1171–1181.

INGRAM, T., STUTZ, W.E. & BOLNICK, D.I. (2011) Does intraspecific size variation in a predator affect its diet diversity and top-down control of prey? *PLoS ONE* **6**, e20782.

JOHANSSON, M., PRIMMER, C.R. & MERILÄ, J. (2007) Does habitat fragmentation reduce fitness and adaptability? A case study of the common frog (*Rana temporaria*). *Molecular Ecology* **16**, 2693–2700.

JOHNSON, M.T.J., LAJEUNESSE, M.J. & AGRAWAL, A.A. (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* **9**, 24–34.

KAWECKI, T.J. & EBERT, D. (2004) Conceptual issues in local adaptation. *Ecology Letters* **7**, 1225–1241.

KEITH, P., PERSAT, H., FEUNTEUN, E. & ALLARDI, J. (2011) *Les poissons d'eau douce de France.* Muséum National d'Histoire Naturelle and Publications Biotope. Paris and Mèze.

KETTLEWELL, H.B.D. (1983) *The evolution of melanism: the study of a recuring necessity; with special reference to industrial melanism in the Lepidoptera.* Oxford University Press, UK.

KILLEN, S.S., MARRAS, S. & MCKENZIE, D.J. (2011) Fuel, fasting, fear: routine metabolic rate and food deprivation exert synergistic effects on risk-taking in individual juvenile European sea bass. *Journal of Animal Ecology* **80**, 1024–1033.

KILLEN, S.S., MARRAS, S., METCALFE, N.B., MCKENZIE, D.J. & DOMENICI, P. (2013) Environmental stressors alter relationships between physiology and behaviour. *Trends in Ecology & Evolution* **28**, 651–658.

KINGSOLVER, J.G., HOEKSTRA, H.E., HOEKSTRA, J.M., BERRIGAN, D., VIGNIERI, S.N., HILL, C.E., HOANG, A., GIBERT, P. & BEERLI, P. (2001) The Strength of Phenotypic Selection in Natural Populations. *The American Naturalist* **157**, 245–261.

KINGSOLVER, J.G. & PFENNIG, D.W. (2007) Patterns and power of phenotypic selection in nature. *Bioscience* **57**, 561–572.

KORICHEVA, J. & HAYES, D. (2018) The relative importance of plant intraspecific diversity in structuring arthropod communities: A meta-analysis. *Functional Ecology* **32**, 1704–1717.

LANDE, R. (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30**, 314–334.

LAVOREL, S. & GARNIER, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional ecology* **16**, 545–556.

LEAL, M.C., BEST, R.J., DURSTON, D., EL-SABAAWI, R.W. & MATTHEWS, B. (2017) Stoichiometric traits of stickleback: Effects of genetic background, rearing environment, and ontogeny. *Ecology and Evolution* **7**, 2617–2625.

LEAL, M.C., SEEHAUSEN, O. & MATTHEWS, B. (2016) The ecology and evolution of stoichiometric phenotypes. *Trends in Ecology & Evolution*.

LECERF, A. & CHAUVET, E. (2008) Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology* **9**, 598–605.

LEINONEN, T., MCCAIRNS, R.J.S., O'HARA, R.B. & MERILÄ, J. (2013) QST–FST comparisons: evolutionary and ecological insights from genomic heterogeneity. *Nature Reviews Genetics* **14**, 179–190.

LEPRIEUR, F., BEAUCHARD, O., BLANCHET, S., OBERDORFF, T. & BROSSE, S. (2008) Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biology* **6**, e28.

LUCEK, K., SIVASUNDAR, A. & SEEHAUSEN, O. (2012) Evidence of adaptive evolutionary divergence during biological invasion. *PLoS ONE* **7**, e49377.

MADRITCH, M., DONALDSON, J.R. & LINDROTH, R.L. (2006) Genetic identity of Populus tremuloides litter influences decomposition and nutrient release in a mixed forest stand. *Ecosystems* **9**, 528–537.

MAGURRAN, A.E. (1990) The inheritance and development of minnow anti-predator behaviour. *Animal Behaviour* **39**, 834–842.

MAGURRAN, A.E. (2004) *Measuring biological diversity*. Blackwell Science Ltd, Oxford, U.K.

MAGURRAN, A.E. (2010) Acquired recognition of predator odour in the European minnow (*Phoxinus phoxinus*). *Ethology* **82**, 216–223.

MAGURRAN, A.E. & PITCHER, T.J. (1987) Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. *Proceedings of the Royal Society B: Biological Sciences* **229**, 439–465.

MATTHEWS, B., AEBISCHER, T., SULLAM, K.E., LUNDSGAARD-HANSEN, B. & SEEHAUSEN, O. (2016) Experimental evidence of an eco-evolutionary feedback during adaptive divergence. *Current Biology* **26**, 483–489.

MATTHEWS, B., DE MEESTER, L., JONES, C.G., IBELINGS, B.W., BOUMA, T.J., NUUTINEN, V., DE KOPPEL, J. VAN & ODLING-SMEE, J. (2014) Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs* **84**, 245–263.

MATTHEWS, B., NARWANI, A., HAUSCH, S., NONAKA, E., PETER, H., YAMAMICHI, M., SULLAM, K.E., BIRD, K.C., THOMAS, M.K., HANLEY, T.C. & TURNER, C.B. (2011) Toward an integration of evolutionary biology and ecosystem science. *Ecology Letters* **14**, 690–701.

MCGILL, B., ENQUIST, B., WEIHER, E. & WESTOBY, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* **21**, 178–185.

MIMURA, M., YAHARA, T., FAITH, D.P., VÁZQUEZ-DOMÍNGUEZ, E., COLAUTTI, R.I., ARAKI, H., JAVADI, F., NÚÑEZ-FARFÁN, J., MORI, A.S., ZHOU, S., HOLLINGSWORTH, P.M., NEAVES, L.E., FUKANO, Y., SMITH, G.F., SATO, Y.-I., ET AL. (2016) Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evolutionary Applications* **10**, 121–139.

MIRÓ, A., SABÁS, I. & VENTURA, M. (2018) Large negative effect of non-native trout and minnows on Pyrenean lake amphibians. *Biological Conservation* **218**, 144–153.

MITTELBACH, G.G., BALLEW, N.G., KJELVIK, M.K. & FRASER, D. (2014) Fish behavioral types and their ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* **71**, 927–944.

MUSETH, J., HESTHAGEN, T., SANDLUND, O.T., THORSTAD, E.B. & UGEDAL, O. (2007) The history of the minnow *Phoxinus phoxinus* (L.) in Norway: from harmless species to pest. *Journal of Fish Biology* **71**, 184–195.

NAEEM, S., BUNKER, D.E., HECTOR, A., LOREAU, M. & PERRINGS, C. (2009) *Biodiversity, Ecosystem Functioning, and Human Wellbeing*. Oxford University Press.

NAEEM, S., THOMPSON, LINDSEY J, LAWLER, SHARON P, LAWTON, JOHN H & WOODFIN, RICHARD M (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* **368**, 734–737.

NAEEM, S. & WRIGHT, J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* **6**, 567–579.

NELSON, J.S., GRANDE, T.C. & WILSON, M.V.H. (1994) *Fishes of the world*. John Wiley and Sons, New York.

NORKKO, A., VILLNAS, A., NORKKO, J., VALANKO, S. & PILDITCH, C. (2013) Size matters: implications of the loss of large individuals for ecosystem function. *Scientific Reports* **3**, 2646.

ODLING-SMEE, J., ERWIN, D.H., PALKOVACS, E.P., FELDMAN, M.W. & LALAND, K.N. (2013) Niche construction theory: a practical guide for ecologists. *The Quarterly Review of Biology* **88**, 3–28.

ODLING-SMEE, J., LALAND, K.N. & FELDMAN, M.W. (2003) *Niche construction the neglected process in evolution.* Princeton University Press. Princeton, NJ.

PAKKASMAA, S. & PIIRONEN, J. (2000) Water velocity shapes juvenile salmonids. *Evolutionary Ecology* **14**, 721–730.

PALKOVACS, E.P., FRYXELL, D.C., TURLEY, N.E. & POST, D.M. (2015) Ecological effects of intraspecific consumer biodiversity for aquatic communities and ecosystems. In *Aquatic Functional Biodiversity*. Elsevier.

PALKOVACS, E.P., MORITSCH, M.M., CONTOLINI, G.M. & PELLETIER, F. (2018) Ecology of harvest-driven trait changes and implications for ecosystem management. *Frontiers in Ecology and the Environment* **16**, 20–28.

PARMESAN, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**, 637–669.

PAZ-VINAS, I. & BLANCHET, S. (2015) Dendritic connectivity shapes spatial patterns of genetic diversity: a simulation-based study. *Journal of Evolutionary Biology* **28**, 986–994.

PAZ-VINAS, I., LOOT, G., STEVENS, V.M. & BLANCHET, S. (2015) Evolutionary processes driving spatial patterns of intraspecific genetic diversity in river ecosystems. *Molecular Ecology* **24**, 4586–4604.

PEARCE, D. (1998) Auditing the earth: the value of the worlds ecosystem services and natural capital. *Environment*, 23–27.

PEIMAN, K.S. & ROBINSON, B.W. (2017) Comparative analyses of phenotypic trait covariation within and among populations. *The American Naturalist* **190**, 451–468.

PELLETIER, F., GARANT, D. & HENDRY, A.P. (2009) Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1483–1489.

PETCHEY, O.L. & GASTON, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* **9**, 741–758.

PIMM, L. (1995) The Future of Biodiversity. *Science* **269**, 4.

PITCHER, T.J. & HOLLINGWORTH, C. (2008) *Recreational fisheries: ecological, economic and social evaluation.* Blackwell Science.

POST, D.M., PALKOVACS, E.P., SCHIELKE, E.G. & DODSON, S.I. (2008) Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology* **89**, 2019–2032.

PRUNIER, J.G., DUBUT, V., LOOT, G., TUDESQUE, L. & BLANCHET, S. (2018) The relative contribution of river network structure and anthropogenic stressors to spatial patterns of genetic diversity in two freshwater fishes: A multiple-stressors approach. *Freshwater Biology* **63**, 6–21.

PURVIS, A. & HECTOR, A. (2000) Getting the measure of biodiversity. *Nature* **405**, 212–219.

REALE, D., GARANT, D., HUMPHRIES, M.M., BERGERON, P., CAREAU, V. & MONTIGLIO, P.-O. (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 4051–4063.

RÉALE, D., READER, S.M., SOL, D., MCDOUGALL, P.T. & DINGEMANSE, N.J. (2007) Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**, 291–318.

ROFF, D.A. (1992) *The evolution of life histories. Theory and analysis*. New York, NY: Chapman & Hall.

ROSENBLATT, A.E. & SCHMITZ, O.J. (2016) Climate change, nutrition, and bottom-up and top-down food web processes. *Trends in Ecology & Evolution*.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013a) Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology* **94**, 1046–1056.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013b) Population structure determines functional differences among species and ecosystem processes. *Nature Communications* **4**.

RUDOLF, V.H.W., RASMUSSEN, N.L., DIBBLE, C.J. & VAN ALLEN, B.G. (2014) Resolving the roles of body size and species identity in driving functional diversity. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20133203.

DE RUITER, P.C., NEUTEL, A.-M. & MOORE, J.C. (1995) Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems. *Science* **269**, 1257–1260.

SCHMITZ, O.J. (2013) Global climate change and the evolutionary ecology of ecosystem functioning. *Annals of the New York Academy of Sciences*, n/a-n/a.

SCHMITZ, O.J., HAWLENA, D. & TRUSSELL, G.C. (2010) Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13**, 1199–1209.

SCHMITZ, O.J., RAYMOND, P.A., ESTES, J.A., KURZ, W.A., HOLTGRIEVE, G.W., RITCHIE, M.E., SCHINDLER, D.E., SPIVAK, A.C., WILSON, R.W., BRADFORD, M.A., CHRISTENSEN, V., DEEGAN, L., SMETACEK, V., VANNI, M.J. & WILMERS, C.C. (2014) Animating the carbon cycle. *Ecosystems* **17**, 344–359.

SCHOENER, T.W. (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* **331**, 426–429.

SEXTON, J.P., HANGARTNER, S.B. & HOFFMANN, A.A. (2014) Genetic isolation by environment or distance: which pattern of gene flow is most common? *Evolution* **68**, 1–15.

SHURIN, J.B., BORER, E.T., SEABLOOM, E.W., ANDERSON, K., BLANCHETTE, C.A., BROITMAN, B., COOPER, S.D. & HALPERN, B.S. (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecology letters* **5**, 785–791.

SHURIN, J.B., GRUNER, D.S. & HILLEBRAND, H. (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B: Biological Sciences* **273**, 1–9.

SIEFERT, A., VIOLLE, C., CHALMANDRIER, L., ALBERT, C.H., TAUDIERE, A., FAJARDO, A., AARSSEN, L.W., BARALOTO, C., CARLUCCI, M.B., CIANCIARUSO, M.V., DE L. DANTAS, V., DE BELLO, F., DUARTE, L.D.S., FONSECA, C.R., FRESCHET, G.T., ET AL. (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**, 1406–1419.

SIH, A., BELL, A. & JOHNSON, J.C. (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**, 372–378.

SKULASON, S. & SMITH, T.B. (1995) Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution* **10**, 366–370.

SLATKIN, M. (1985) Gene flow in natural populations. *Annual Review of Ecology and Systematics* **16**, 393–430.

SMITH, T.B. & SKULASON, S. (1996) Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics* **2**, 111–133.

STOMP, M., HUISMAN, J., MITTELBACH, G.G., LITCHMAN, E. & KLAUSMEIER, C.A. (2011) Large-scale biodiversity patterns in freshwater phytoplankton. *Ecology* **92**, 2096–2107.

STRAYER, D.L. & DUDGEON, D. (2010) Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society* **29**, 344–358.

TERBORGH, J. & ESTES, J.A. (2010) *Trophic cascades: predators, prey and the changing dynamics of nature.* Island Press, Washington DC.

THÉBAULT, E. & LOREAU, M. (2005) Trophic Interactions and the Relationship between Species Diversity and Ecosystem Stability. *The American Naturalist* **166**, E95–E114.

THOMPSON, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology & Evolution* **13**, 329–332.

TILMAN, D., KNOPS, J.M.H., WEDIN, D., REICH, P.B., RITCHIE, M.E. & SIEMANN, E. (1997) The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science* **277**, 1300–1302.

TILMAN, D., REICH, P.B. & KNOPS, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632.

TORRES-DOWDALL, J., HANDELSMAN, C.A., REZNICK, D.N. & GHALAMBOR, C.K. (2012) Local adaptation and the evolution of phenotypic plasticity in trinidian guppies (*Poecilia reticulata*). *Evolution* **66**, 3432–3443.

TURCOTTE, M.M., REZNICK, D.N. & DANIEL HARE, J. (2013) Experimental test of an eco-evolutionary dynamic feedback loop between evolution and population density in the green peach aphid. *The American Naturalist* **181**, S46–S57.

UTSUMI, S. (2015) Feeding evolution of a herbivore influences an arthropod community through plants: implications for plant-mediated eco-evolutionary feedback loop. *Journal of Ecology* **103**, 829–839.

VANNI, M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* **33**, 341–370.

VANNOTE, R.K., MINSHALL, G.W., CUMMINS, K.W., SEDELL, J.R. & CUSHING, C.E. (1980) The River continuum concept. *Canadian Journal of Zoology* **37**, 130–137.

VELLEND, M. (2003) Island biogeography of genes and species. *The American Naturalist* **162**, 358–365.

VELLEND, M. (2005) Species diversity and genetic diversity: parallel processes and correlated patterns. *The American Naturalist* **166**, 199–215.

VELLEND, M. & GEBER, M.A. (2005) Connections between species diversity and genetic diversity. *Ecology Letters* **8**, 767–781.

VILLÉGER, S., BROSSE, S., MOUCHET, M., MOUILLOT, D. & VANNI, M.J. (2017) Functional ecology of fish: current approaches and future challenges. *Aquatic Sciences* **79**, 783–801.

VIOLLE, C., ENQUIST, B.J., MCGILL, B.J., JIANG, L., ALBERT, C.H., HULSHOF, C., JUNG, V. & MESSIER, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* **27**, 244–252.

VIOLLE, C., NAVAS, M.-L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. & GARNIER, E. (2007) Let the concept of trait be functional! *Oikos* **116**, 882–892.

VÖRÖSMARTY, C.J., MCINTYRE, P.B., GESSNER, M.O., DUDGEON, D., PRUSEVICH, A., GREEN, P., GLIDDEN, S., BUNN, S.E., SULLIVAN, C.A., LIERMANN, C.R. & DAVIES, P.M. (2010) Global threats to human water security and river biodiversity. *Nature* **467**, 555–561.

WALSH, M.R., DELONG, J.P., HANLEY, T.C. & POST, D.M. (2012) A cascade of evolutionary change alters consumer-resource dynamics and ecosystem function. *Proceedings of the Royal Society B-Biological Sciences* **279**, 3184–3192.

WANG, X.-Y., MIAO, Y., YU, S., CHEN, X.-Y. & SCHMID, B. (2014) Genotypic diversity of an invasive plant species promotes litter decomposition and associated processes. *Oecologia* **174**, 993–1005.

WARDLE, D.A. (1999) Is 'sampling effect' a problem for experiments investigating biodiversity-ecosystem function relationships? *Oikos* **87**, 403.

WARDLE, D.A., BONNER, K.I. & NICHOLSON, K.S. (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* **79**, 247.

WETZEL, R.G. (1995) Death, detritus, and energy flow in aquatic ecosystems. *Freshwater Biology* **33**, 83–89.

WHITHAM, T.G., BAILEY, J.K., SCHWEITZER, J.A., SHUSTER, S.M., BANGERT, R.K., LEROY, C.J., LONSDORF, E.V., ALLAN, G.J., DIFAZIO, S.P., POTTS, B.M., FISCHER, D.G., GEHRING, C.A., LINDROTH, R.L., MARKS, J.C., HART, S.C., ET AL. (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* **7**, 510–523.

WHITHAM, T.G., DIFAZIO, S.P., SCHWEITZER, J.A., SHUSTER, S.M., ALLEN, G.J., BAILEY, J.K. & WOOLBRIGHT, S.A. (2008) Extending genomics to natural communities and ecosystems. *Science* **320**, 492–495.

WHITHAM, T.G., YOUNG, W.P., MARTINSEN, G.D., GEHRING, C.A., SCHWEITZER, J.A., SHUSTER, S.M., WIMP, G.M., FISCHER, D.G., BAILEY, J.K., LINDROTH, R.L., WOOLBRIGHT, S. & KUSKE, C. (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* **84**, 559–573.

WOODWARD, G., EBENMAN, B., EMMERSON, M., MONTOYA, J., OLESEN, J., VALIDO, A. & WARREN, P. (2005) Body size in ecological networks. *Trends in Ecology & Evolution* **20**, 402–409.

YVON-DUROCHER, G., ALLEN, A.P., CELLAMARE, M., DOSSENA, M., GASTON, K.J., LEITAO, M., MONTOYA, J.M., REUMAN, D.C., WOODWARD, G. & TRIMMER, M. (2015) Five years of experimental warming increases the biodiversity and productivity of phytoplankton. *PLoS Biol* **13**, e1002324.

ZANDEN, M.J.V., SHUTER, B.J., LESTER, N.P. & RASMUSSEN, J.B. (2000) Within- and among-population variation in the trophic position of a pelagic predator, lake trout **57**, 7.

ZANDONÀ, E., DALTON, C.M., EL-SABAAWI, R.W., HOWARD, J.L., MARSHALL, M.C., KILHAM, S.S., REZNICK, D.N., TRAVIS, J., KOHLER, T.J., FLECKER, A.S., THOMAS, S.A. & PRINGLE, C.M. (2017) Population variation in the trophic niche of the Trinidadian guppy from different predation regimes. *Scientific Reports* **7**, 5770.

ZAVORKA, L., KOECK, B., CUCHEROUSSET, J., BRIJS, J., JOACIM NÄSLUND, ALDVÉN, D., HÖJESJÖ, J., FLEMING, I.A. & JOHNSSON, J.I. (2017) Co-existence with non-native brook trout breaks down the integration of phenotypic traits in brown trout parr. *Functional Ecology* **31**, 1582–1591.

ZÁVORKA, L., LANG, I., RAFFARD, A., EVANGELISTA, C., BRITTON, J.R., OLDEN, J.D. & CUCHEROUSSET, J. (2018) Importance of harvest-driven trait changes for invasive species management. *Frontiers in Ecology and the Environment* **16**, 317–318.

ANNEXE 1 The Functional Syndrome: linking individual trait variability to ecosystem functioning

Raffard Allan[1,2,3], Lecerf Antoine[2], Cote Julien[1], Buoro Mathieu[1,3], Lassus Remy[1], & Cucherousset Julien[1]

[1] *CNRS, Université Toulouse III Paul Sabatier, Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UMR-5321, F-09200 Moulis, France.*

[2] *EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France.*

[3] *Laboratoire Évolution et Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, IRD, UPS, 118 route de Narbonne, Toulouse 31062, France.*

[4] *ECOBIOP, INRA, Univ.Pau and Pays Adour, 64310 St Pée-sur-Nivelle, France*

Manuscript published in **Proceedings of the Royal Society B**.

Résumé

La variabilité phénotypique est de plus en plus quantifiée au travers des traits réponses et d'effets. Cela permet d'étudier les mécanismes par lesquels les organismes répondent aux variations environnementales et affectent le fonctionnement des écosystèmes. Peu de travaux se sont intéressés aux covariations entre les traits réponses et effets, ce qui limite la compréhension des effets écosystémiques de la variabilité phénotypique. Durant une période de neuf mois, nous avons mesuré plusieurs traits sur des écrevisses de Louisiane (*Procambarus clarkii*), et nous avons démontré que la majorité des traits étudiés étaient stables durant l'ontogénie des individus. Des ensembles de traits réponses et effets étaient associés respectivement avec un syndrome réponse et un syndrome effet, qui étaient corrélés entre eux formant un syndrome fonctionnel. En utilisant un modèle bioénergétique, nous avons prédit que des populations avec des différences de syndrome réponse pouvaient avoir un impact sur le taux de décomposition aussi fort que les effets induits par un doublement de la taille de population. La définition d'un syndrome fonctionnel peut améliorer la compréhension des impacts écologiques de la variabilité phénotypique entre individus, et des liens entre l'écologie des écosystèmes et évolutive.

Abstract

Phenotypic variability is increasingly assessed through functional response and effect traits, which provide a mechanistic framework for investigating how an organism responds to varying ecological factors and how these responses affect ecosystem functioning. Covariation between response and effect traits has been poorly examined at the intraspecific level, thus hampering progress in understanding how phenotypic variability alters the role of organisms in ecosystems. Using a multi-trait approach and a nine month longitudinal monitoring of individual red-swamp crayfish (*Procambarus clarkii*), we demonstrated that most of the measured response and effect traits were partially stable during the ontogeny of individuals. Suites of response and effect traits were associated with a response syndrome and an effect syndrome, respectively, which were correlated to form a functional syndrome. Using a bioenergetic model, we predicted that differences in the response syndrome composition of hypothetical populations had important ecological effects on a key ecosystem process (i.e. whole-lake litter decomposition) to a level similar to those induced by doubling population size. Demonstrating the existence of a functional syndrome is likely to improve our understanding of the ecological impacts of phenotypic variation among individuals in wild populations across levels of biological organisation, and the linkage between ecosystem and evolutionary ecology.

Introduction

While trait variability among individuals has been historically accounted for in evolutionary sciences, it has merely been seen merely as noise around the average phenotype of a species by community and ecosystem ecologists (Bolnick *et al.*, 2003, 2011; Violle *et al.*, 2012). Recent advances have, however, suggested that not only organism phenotypes are affected by their environment, but that they can reciprocally act on it (Odling-Smee, Laland, & Feldman, 2003; Bolnick *et al.*, 2011), coupling ecological and evolutionary processes in a dynamic relationship (Pelletier, Garant, & Hendry, 2009; Matthews *et al.*, 2014; Hendry, 2016). In this context, the ecological consequences of interindividual variability are increasingly recognised, and recent studies have demonstrated broad consequences of phenotypic variability on key ecosystem processes such as primary production and leaf litter decomposition (Bassar *et al.*, 2010; Rudolf & Rasmussen, 2013a, 2013b; El-Sabaawi *et al.*, 2015a). To date, however, most studies have focused on the ecosystem effects of a single phenotypic trait (e.g. morphology, body mass) despite the fact that individuals can simultaneously vary in multiple phenotypic traits (Sih, Bell, & Johnson, 2004) (but see for instance (Bassar *et al.*, 2010)). Therefore, a multi-trait approach is needed to provide an integrative understanding of the effects of individuals on ecosystems.

From a functional perspective, phenotypic traits have been classified as functional effect traits or functional response traits (Violle *et al.*, 2007; Díaz *et al.*, 2013). On one hand, functional effect traits determine how and to what extent an organism influences energy flow and matter transformation in an ecosystem (Díaz *et al.*, 2013). For instance, nitrogen excretion rate is considered as an effect trait because it induces changes in nutrient availability resulting in altered algal growth, thus modifying primary productivity (El-Sabaawi *et al.*, 2015b). On the other hand, functional response traits determine how an organism responds to environmental conditions (Violle *et al.*, 2007; Díaz *et al.*, 2013). For instance, presence of predators may reduce individual activity (Wooster & Sih, 1995), therefore activity level is considered as a response trait. Studies linking intraspecific trait variability to ecosystem functioning have mostly focused on response trait variations [e.g. sex ratio (Fryxell *et al.*, 2015), morphology (Harmon *et al.*, 2009) or behaviour (Royauté & Pruitt, 2015)]. However, response traits and ecosystem processes are not proximately related and, therefore, such relationships are conditional on covariations between response and effect traits. For instance, phenotypic variations in guppies (*Poecilia reticuata*) has been demonstrated to impact primary productivity through a correlation between individual life history and nitrogen excretion rate (Bassar *et al.*, 2010).

Evolutionary biologists have shed light on various patterns of covariations in life history and behavioural traits. These correlations among phenotypic traits are termed *syndrome*, including the life history and behavioural syndromes (Roff, 1992; Sih *et al.*, 2004). The 'Pace Of Life Syndrome' hypothesis further states that trait covariation extends over several phenotypic aspects including the life history, behaviour and physiology of organisms (Reale *et al.*, 2010). These syndromes are best understood as having emerged from evolutionary processes and, therefore, lack relevance to infer the relationship between response and effect traits which are underlined in eco-evolutionary dynamics (Pelletier *et al.*, 2009; Hendry, 2016). This leads us to introduce the concept of 'functional syndrome' which we define as the association between correlated suites of response and effect traits (i.e. between a 'response syndrome' and an 'effect syndrome', Figure 1). The dependence of effect traits upon response traits may arise from metabolic and stoichiometric constraints (metabolic theory of ecology, Brown *et al.*, 2004; Leal, Seehausen, & Matthews, 2016). For instance, fast-paced individuals with high metabolic and nutrient requirements are expected to exert stronger top-down control on their resources than slow-growing individuals. Nutrient immobilization - contributing to growth rate - may result in a slower rate of nutrient excretion of fast-paced individuals than slow-paced individuals (Leal, *et al.*, 2016).

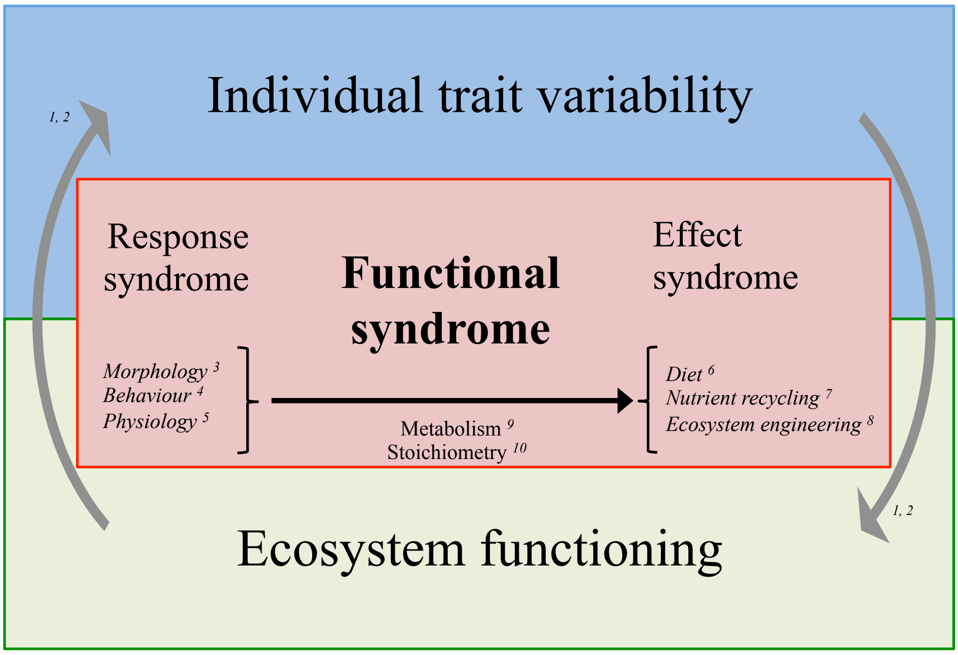

Figure 1. Conceptual representation of the functional syndrome. Association between response and effect traits (represented by the central arrow) is at the core of the interactions between individual trait variability and ecosystem functioning that are linked through eco-evolutionary dynamics (represented by the grey arrows). Examples of categories of response traits (through which individuals adapt to their environment) and of effect traits (by which individuals act on their ecosystem) are provided under their respective syndrome. The superscripts refer to cited references. Superscripts indicate references: 1. Pelletier et al., 2009; 2. Hendry, 2016; 3. Harmon et al., 2009; 4. Biro, Adriaenssens, & Sampson, 2014; 5. Ketterson, Atwell, & McGlothlin, 2009; 6. Bolnick et al., 2003; 7. Vanni, 2002; 8. Matthews et al., 2014; 9. Brown et al., 2004; 10. Leal, et al., 2016.

The aim of the present study was to test the existence of a functional syndrome linking functional response and effect traits and to use this association to predict the effects of intraspecific variability on ecosystem functioning. Using the red-swamp crayfish (*Procambarus clarkii*) as the model species, we monitored individuals longitudinally (9 months) and repeatedly quantified several response and effect traits. We then applied a mass-balance bioenergetic model in a Bayesian framework to predict the ecosystem consequences of hypothetical populations varying in their phenotypic traits. First, we tested the hypotheses that *i*) response traits (boldness, anxiety, chelae morphology and growth rate) were consistent over time and correlated to form a response syndrome and that *ii*) effect traits (voracity, predation rate, leaf consumption rate, egestion rate and ammonium excretion rate) were also consistent over time and correlated to form an effect syndrome. Second, we tested the hypothesis that the response and effect syndromes were associated to form a functional syndrome. Because traits were quantified across several ontogenetic stages, we also tested the body mass independency of these associations. Third, we simulated hypothetical populations differing in size and response syndrome composition to predict ecosystem consequences (whole-lake litter decomposition dynamics).

Materials and methods

Model species

Native to North and Central America, the red-swamp crayfish has been introduced and established throughout Europe (Gherardi, 2006). Described as an opportunistic and omnivorous species, it is considered an ecosystem engineer and its ecological impacts include decreased macrophyte biomass through direct consumption (Gherardi, 2006), increased water turbidity driven by burrowing behaviour (Twardochleb, Olden, & Larson, 2013) and changes in the phenology of litter decomposition (Alp *et al.*, 2016). Importantly, it has been demonstrated to display anxiety-like behaviour (Fossat *et al.*, 2014).

Animal rearing and experimental design

In June 2014, 240 juveniles (carapace length range: 20.95 mm – 35.14 mm) were collected from a single population (Lake Lamartine, south-western France, 43°30'21.5"N, 1°20'32.7"E). To avoid any behavioural bias caused by the sampling method (Biro & Dingemanse, 2009), individuals were captured using several active and passive methods in all habitats of the lake. In the laboratory, we maintained crayfish in 50 L tanks and marked them individually using PIT (Passive Integrated Transponder) tags (8 × 1.4 mm, FDX-B 'skinny' PIT tag, Oregon RFID, USA), inserted at the base of the fifth pereiopod pair through an incision made with a sterile scalpel (Bubb *et al.*, 2002). Sixty-four individuals were chosen for the experiment to maximize interindividual variability based on boldness measurements performed in July 2014. For selection, we classified individuals into three categories (supplementary materials) and randomly picked 20 individuals from each category (and 2 extra individuals from the extreme categories). We chose to maximize interindividual variability in order to increase our statistical power to detect existing correlations among traits. The experiment lasted 289 days (see supplementary materials for rearing conditions) and a total of 55 individuals survived.

Functional trait measurements

Response traits

Boldness and anxiety-like behaviour were assessed six times (see details in Table S1 and Figure S1) using corridors covered with 2 cm of sand at the bottom and filled with 37.5 L of dechlorinated tap water and 2 L of water from tanks with conspecifics. The corridors (Figure S2) contained two dark areas separated by a light area. Each corridor (n = 5) was separated by opaque walls to avoid visual contact between individuals and surrounded by curtains to obtain homogeneous light conditions. Individuals were first acclimated for 20 min in an opaque container to reduce stress level induced by handling. After being gently released in one of the dark areas for 10 min of acclimation, the sliding door was opened and individuals were filmed for 10 min. Video footage were subsequently analysed using "Observer" (Noldus Information Technology, Wageningen, the Netherlands). Boldness was quantified as the time before emergence from the acclimation area. We inversed the scores to associate higher values with higher boldness (Cote *et al.*, 2010). Anxiety-like behaviour was assessed as the proportion of time spent in dark zones after original emergence from the acclimation zone, representing a stress avoidance behaviour (Fossat *et al.*, 2014). The order and the corridor in which individuals were assayed were randomly attributed at the first trial and were fixed for all repetitions. All behavioural assays were performed in the morning (08:00-12:00) to minimize the potential effects of circadian rhythms. Individuals were starved for two days prior to each behavioural assay.

Chelae are extremely important and costly organs for crayfish (Stein, 1976) and chelae morphology was selected as a response trait because they are used for individual defence against predators and competition with conspecifics (Pintor, Sih, & Bauer, 2008). Although they require a higher energy investment, large and arched chelae are stronger (Claverie & Smith, 2007). Chelae morphology was quantified using two complementary approaches: morphometric ratio and shape determination using landmark coordinates. Individual right chela and body were pictured and measurements (chela length CLL, carapace length CL, chela width CW and palm length PL) were performed using ImageJ. Morphometric ratios that represent energy allocation to the chelae (CLL/CL) and chelae relative width (CW/PL; CW/CL) were then calculated (Larson *et al.*, 2012). We digitalized 7 landmarks (adapted from (Claverie & Smith, 2007) using TpsDig2 (Rohlf, 2005)) to evaluate chelae shape. A principal component analysis (PCA, package ade4 on R, Chessel, Dufour, & Dray, 2007; R Core Team, 2013) was performed on partial warp scores (TpsRelw) to obtain a chelae shape score for each individual. A second PCA was then performed on residuals of morphometric ratios with sex (because of potential sexual dimorphism) and chelae shape to obtain an integrative score of chelae morphology.

Growth rate is strongly dependent on individual food intake, metabolism and assimilation efficiency of nutrients and was quantified six times by weighing individuals (nearest 0.01 g) on seven occasions (Figure S1). Specific growth rate (SGR, %.day^{-1}) was calculated as:

$$SGR = \frac{ln(Wf) - ln(Wi)}{T} * 100$$

where Wf and Wi were the final and initial body mass, respectively, and T the time interval between two measurements, expressed in days.

Effect traits

Predation rate is an important effect trait since it can impact ecosystem functioning (e.g. trophic cascade). Predation was quantified using individual containers filled with 2.5 L of dechlorinated tap water and 20 unfrozen chironomids per container. Chironomids were selected because they are one of the most abundant littoral invertebrates in the study area and are commonly consumed by red swamp crayfish outside of its native range (Alcorlo, Geiger, & Otero, 2004). Commercially-available frozen chironomids were purchased at the start of the experiment to ensure that all measurements of predation were performed using prey similar in size and origin throughout the experiment. After 10 min of acclimation, individuals were allowed to access the chironomids for 10 min. Individuals were then removed and the number of remaining chironomids was counted. Predation rate was quantified twice for each individual at the beginning of the experiment (Figure S1) when individuals were the youngest since juveniles have a more carnivorous diet than sub-adults (Correia, 2003). Hunger state was controlled by starving individuals for two days before experimentation.

Voracity, i.e. individual foraging activity (Pintor *et al.*, 2008) associated with individual behaviour and physiology, was quantified nine times for each individual, in the home tank at 09:00, three times per week during three consecutives weeks (Figure S1). Individuals were starved for 2 days before each measurement. The voracity test consisted of introducing four pellets of food in each tank and quantifying the number of pellets consumed after 20 min. We cumulated the scores for each week to obtain 3 measurements of voracity.

Leaf consumption and egestion rates were used as relevant effect traits depicting crayfish impacts on detritus dynamics and carbon cycle (Gessner, Chauvet, & Dobson, 1999). Consumption reduces stock of coarse particulate organic matter (Alp *et al.*, 2016) while egestion of faeces enhances nutrient recycling by microorganisms (Wotton & Malmqvist, 2001). Consumption rate ($g.d^{-1}$) of abscised leaves of black poplar (*Populus nigra*) was quantified three times (Figure S1) for each individual. Prior to the experiment, leaves were submerged for 2 weeks in a pond to allow microbial conditioning, a process that improves leaf palatability to detritivores (Lecerf *et al.*, 2005). Batches of air-dried leaves (4.0 g) were enclosed in 0.5-mm nylon mesh bags to prevent invertebrates in the pond from accessing the leaves. At retrieval, the leaves were rinsed with demineralized water to remove fine sediments. Crayfish were placed in container filled with 2.5 L of dechlorinated tap water with an air stone for oxygenation. After 5 h of acclimation, conditioned leaves were introduced and left for 72 h. The remaining leaf material was then oven dried at 70°C for 48 h and subsequently weighed to the nearest 0.01 g. Five controls without crayfish were used to quantify leaf mass loss due to microbial decomposition and leaching; this mass loss was accounted for when calculating crayfish consumption rate. Water from each container was filtered through two sieves: 1 mm mesh size to remove small leaf fragments and 50 µm mesh size to collect the faeces released by crayfish. The faecal matter was oven dried at 60°C for 72 h and weighed to the nearest 0.01 mg. Egestion rate was expressed in grams per day.

Nitrogen excretion rate was quantified by measuring excretion of dissolved ammonium NH_4^+, which is a metabolic waste produced during the breakdown of proteins and amino-acids (Freire, Onken, & McNamara, 2008). Changes in NH_4^+ concentration can affect ecosystem functioning through an increase in nutrient availability (Capps & Flecker, 2013) and primary production (Vanni, 2002; Schmitz, Hawlena, & Trussell, 2010). Excretion rate was quantified three times for each individual (Figure S1). All individuals were fed *ad libitum* the day before and 2 hours prior to the start of the excretion experiment by adding 3 pellets to each tank. Individuals were then placed in plastic bags containing 500 ml of spring bottled water for 2h (Villéger *et al.*, 2012). Individuals were then removed and 100 ml of water was filtered through a glass microfiber filter (Whatman, GF/C, diameter = 25 mm) and samples were frozen at -20°C. Excretion rate (NH_4^+, $mg.l^{-1}.h^{-1}$) was determined using a high-performance ionic chromatograph (Dionex DX-120).

Statistical analysis and modelling

Response trait syndrome

First we assessed the level of individual repeatability of each response trait and the correlations among them. Boldness, growth rate, morphology and voracity were measured for a total of 55 individuals. Because some individuals never left the acclimation area, anxiety-like behaviour was measured on 50 individuals. Generalized linear mixed models (package lme4, Bates *et al.*, 2014) were used to test the repeatability of traits using a Gaussian family. For all models, we fitted time as a fixed effect and individuals as a random effect. Additional random effects were included to control for potential sources of variation owing to experimental design (corridor for boldness and anxiety-like behaviour tests and shelf for growth rate). Repeatability was quantified using the Intraclass Coefficient Correlation (Nakagawa & Schielzeth, 2010). The significance of the repeatability (i.e. variance explained by between-individual differences) was tested using a likelihood ratio test by comparing the model with individual as random effect to an alternative model without this random effect.

Correlations among response traits were tested based on averaged trait values calculated across temporal replicates. Boldness, anxiety-like behaviour and growth rate were, however, averaged for repetitions made in 2015 to compare response traits measured at the same time as effect traits. We assessed correlations among response traits using averaged values instead of all repeats. This approach prevents comparing intra- versus inter-individual correlation but, in the present study, not all traits were measured at the same time and we primarily focused on inter-individual correlation. Correlations among response traits were tested using Spearman’s rank correlations.

Effect trait syndrome

Because of moulting, consumption and egestion rates were measured on 52 individuals, excretion rate on 53 and predation rate on 55. The repeatability of effect traits was tested as previously described (shelves used as additional random term). Effect traits were then averaged across temporal replicates and correlations among effect traits were tested using Spearman’s ranks correlations.

Relationship between response and effect traits

We used Partial least squares path modelling (PLS-PM, plspm package, Sanchez, 2013) to summarise the trait covariance structure and to compute latent (i.e. proxy) variables representing response and effect syndromes. This technique is a robust form of structural equation modelling that relies on fewer assumptions than does covariance-based structural equation modelling (Sanchez, 2013; Henseler *et al.*, 2014). PLS-PM is suitable for examining relationships between blocks of associated traits since latent variables are formed as linear combinations of traits without imposing any restrictions on within-block covariances. We constructed a simple path model wherein effect traits were conditioned upon response traits and individual body mass (averaged over 3 measurements) was specified as a mediator of this relationship. Body mass is known to be correlated with both effect and response traits, therefore, some variations in effect traits may be due to differences in crayfish body mass. Standardised path coefficients were used to evaluate the strength of relationships tested in the model. We calculated the product of the path coefficients along the mediation pathway to assess the strength of mass-dependent relationship between response and effect traits. The construction of response and effect syndromes was examined using correlations between traits and the latent variables they form (i.e. loadings). We removed the traits with the lowest contribution to the latent variables (i.e. boldness and predation) to obtain stable and accurate parameter estimates (Sanchez, 2013). Significance was assessed using 95% percentile confidence intervals calculated on 200 bootstrap samples. PLS-PM was performed on a subset of 47 individuals for which no missing trait values occurred.

Modelling consequences on ecosystem functioning

A mass-balance bioenergetic model (Table S2) was used to assess the ecosystem impact of the link between the response and effect traits. Variations among individuals in their consumption rates can act on litter decomposition, a key ecosystem function of freshwater ecosystems (Gessner *et al.*, 1999). As consumption is linked to individual growth rate, population biomass is also associated to response traits. The bioenergetic model was based on individual consumption and was modified to include the link between the response trait syndrome and consumption rate. To do so, we first evaluated the effect of the response syndrome (the latent variable extracted from the PLS-PM) on leaf consumption rate based on experimental data using a linear regression in a Bayesian framework. We then used these outputs (i.e. estimated regression parameters) and projected values of response traits syndrome and daily temperature (Table S2) to simulate growth rate, consumption rate and population biomass over a year using an individual bioenergetic model (see supplementary materials).

Simulations were performed on a sequence of 11 hypothetical populations composed of individuals with different syndrome values sampled along the observed distribution. We also added one control population composed of individuals with fully random syndrome values. Each population was modelled with eleven densities ranging from 1000 to 2000 individuals (simulating a biological invasion process). To estimate the effects of the simulated populations on decomposition rate and population biomass, the environmental factors were sourced from a realistic ecosystem (daily temperature and litter input). The decomposition rate was estimated over one year as $k = -\frac{ln\,(X)}{t}$ (Zhang *et al.*, 2008), where X is the proportion of litter remaining after consumption by the crayfish and t is the time elapsed in years. To assess whether different population induced differences in final biomass, we quantified the difference between biased response trait syndrome and control populations. All statistical analyses were performed using R software (R Core Team, 2013) unless specified otherwise.

Results

Overall, we observed various levels of trait variability among individuals. For instance, mean boldness varied from 44 s (± 32 SD) to 473 s (± 87 SD) across the 55 individuals. Mean anxiety-like behaviour ranged from 0.43 (± 0.05 SD) to 0.74 (± 0.14 SD) and mean voracity ranged from 0.1 (± 0.3 SD) to 4.0 (± 0.0 SD) pellets eaten in 20 min. Growth rate was also variable among individuals, ranging from 0.14 (± 0.34 SD) to 0.63 (± 0.47 SD) $\%.\mathrm{day}^{-1}$. Effect traits also varied among individuals. Predation rate varied from 4.0 (± 5.5 SD) to 17.5 (± 3.5 SD) chironomids eaten in 10 min, leaf consumption rate ranged from 0.00 (± 0.00 SD) to 0.31 (± 0.01 SD) $\mathrm{g.day}^{-1}$, egestion rate ranged from 0.002 (± 0.001 SD) to 0.18 (± 0.033 SD) $\mathrm{g.d}^{-1}$ and excretion rate from 0.05 (± 0.02 SD) to 0.18 (± 0.06 SD) $\mathrm{mg.L}^{-1}.\mathrm{h}^{-1}$.

Response and effect syndromes

Boldness and anxiety-like behaviour were significantly repeatable over 9 months (Table S3, generalized linear mixed model, boldness: ICC = 0.31, $\chi^2 = 49.49$ $p < 0.001$, anxiety-like behaviour: ICC = 0.14, $\chi^2 = 9.67$, $p = 0.002$). However, growth rate was not repeatable (ICC = 0.00, $\chi^2 = 0.00$, $p = 1$). The morphological axis (first PCA axis: 51% of total variance explained) was explained by the energy allocation to chelae compared to the body (loading component: 0.51), chelae width (0.42 and 0.58) and chelae shape (-0.46), i.e. individuals with higher morphological scores had, proportionally to their body, larger, longer and more arched chelae. Morphology was significantly and positively correlated with boldness ($\rho = 0.25$, $p = 0.043$), while boldness and anxiety-like behaviour were negatively correlated ($\rho = -0.30$, $p = 0.034$). Other correlations were non-significant (Table S4).

Predation, consumption rate and voracity were significantly repeatable over time (Table S3, ICC = 0.34, $\chi^2 = 6.86$, $p = 0.009$, ICC = 0.24, $\chi^2 = 8.11$, $p = 0.004$, and ICC = 0.78, $\chi^2 = 114.24$, $p < 0.001$, respectively). Egestion rate was repeatable (ICC = 0.37, $\chi^2 = 19.01$, $p < 0.001$) while ammonium excretion rate was not significantly repeatable (ICC = 0.00, $\chi^2 = 0.00$, $p = 1$). Consumption, egestion and excretion rates were all correlated among each other (consumption-egestion: $\rho = 0.94$, $p < 0.001$, consumption-excretion: $\rho = 0.38$, $p = 0.006$ and egestion-excretion: $\rho = 0.40$, $p = 0.003$; Table S5). Voracity was correlated with the rates of leaf consumption, egestion and excretion ($\rho = 0.65$, $p < 0.001$, $\rho = 0.64$, $p < 0.001$, and $\rho = 0.29$, $p = 0.031$ respectively). Predation rate was not correlated with any other effect traits (Table S5).

Functional syndrome

The latent variable corresponding to the response syndrome was positively associated with growth rate and chelae morphology and negatively with anxiety-like behaviour (Figure 2). The second latent variable correlated with voracity, leaf consumption, egestion and, to a lesser extent, excretion rates to form an effect syndrome (Figure 2). The response syndrome and body mass were positively linked (path coefficient = 0.67, 95% percentile confidence intervals (CI) = [0.45; 0.82], $R^2 = 0.46$). The effect syndrome was directly and positively associated with the response syndrome (path coefficient = 0.40, CI = [0.02; 0.80]) but not with body mass (path coefficient = 0.22, CI = [-0.22; 0.58], $R^2 = 0.37$). This led to an indirect association of response syndrome on effect syndrome with a strength that was not significant and lower than the direct effect (path coefficient = 0.15, CI = [-0.10; 0.48]).

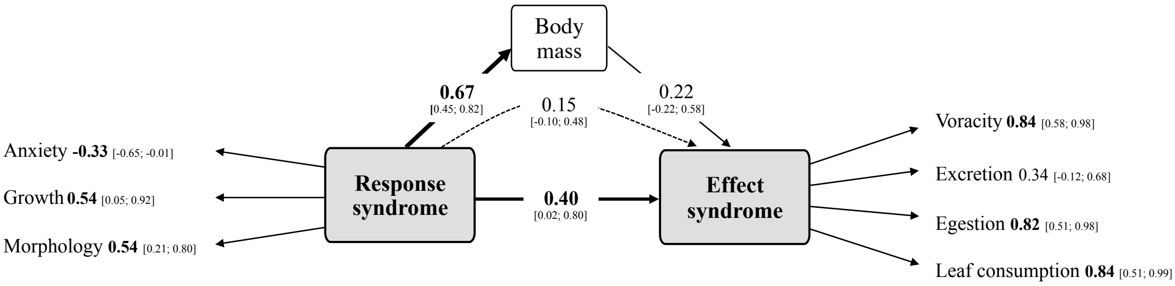

Figure 2. Representation of the partial least squared path modelling (PLS-PM) assessing relationships between response syndrome, body mass and effect syndrome (goodness-of-fit of the overall model = 0.42). The width of arrows connecting boxes is proportional to the mean value of standardised path coefficient (displayed on the arrows). The dashed arrow represents the mass-dependent relationship between the response syndrome and effect syndrome. Its strength was calculated as the product of the path coefficient from the response syndrome to body mass and the path coefficient from body mass to the effect syndrome (i.e. 0.15). Loadings associated with response and effect traits indicate how they contribute to the response and effect syndromes (i.e. latent variable), respectively. Values reported in square brackets represent 95% percentile confidence intervals calculated on 200 bootstrap samples and significant path coefficients and loadings are displayed in bold. Boldness (response trait) and predation (effect trait) were removed from the model due to their weak correlation with their respective latent variable.

Consequences of trait variability on ecosystem functioning

The model predicted that differences in response trait syndrome values induced a change in final population biomass when compared to a control population with individuals with random trait values (Figure 3a). Specifically, population biomass was higher for a population with high response trait syndrome than for the control population while it was lower for a population with low response trait syndrome (Figure 3a). The model also predicted a higher decomposition rate for hypothetical populations with higher response trait values, independent of population density (Figure 3b). The decomposition rate after 1 year was twice as high for populations with high syndrome values compared to populations with low values (Figure 3b). Doubling population size (i.e. from 1000 to 2000 individuals) led to the same effect on decomposition rate than changing from lowest to highest syndrome values. For instance, the decomposition rate for a population composed of 2000 individuals with a low response traits syndrome value was similar to that of a population of 1000 individuals with a high response traits syndrome (k = 0.094 year^{-1}, 95% predictive interval (PI) = [0.058; 0.142] and k = 0.153 year^{-1}, PI= [0.087; 0.295], respectively).

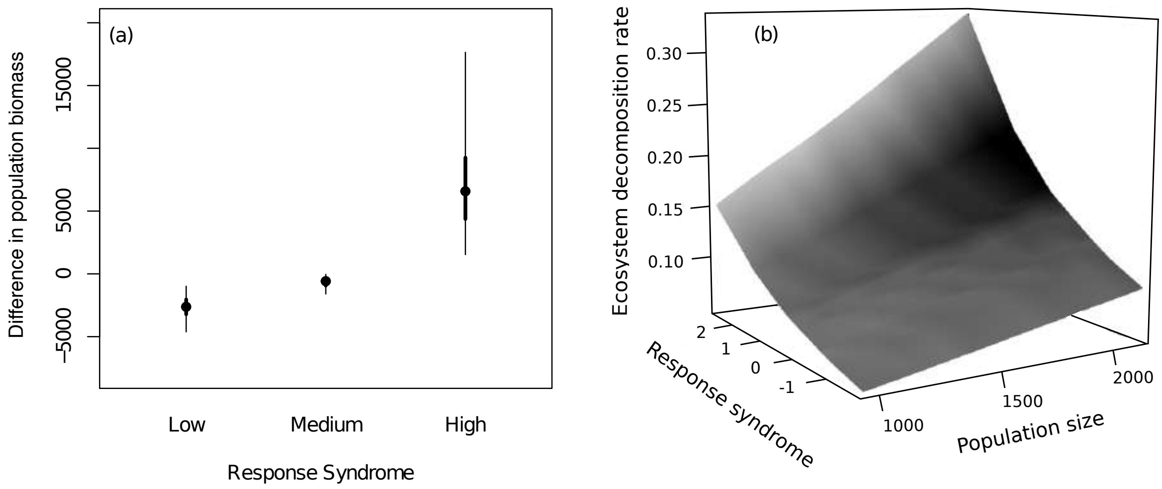

Figure 3. (a) Difference in crayfish biomass between populations composed of individuals with different response syndromes and a control population (random trait values). The thin error bars represent 95 % posterior predictive distribution and the bold error bars represent 50% posterior predictive distribution. **(b)** Three-dimensional representation of the relationship between response syndrome, population size (number of individuals) and decomposition rate (k) based on medians of the posterior predictive distribution.

Discussion

Providing a mechanistic and integrative framework to understand how variations in phenotypic traits affect ecosystem functioning is crucial. Using a multi-trait approach that explicitly integrated functional response and effect traits, we first demonstrated the existence of a response syndrome based on the covariation among a suite of response traits (morphology, growth rate and anxiety-like behaviour). We then found that effect traits (voracity, leaf consumption, egestion and excretion rates) formed an effect syndrome, which was associated with the response syndrome, revealing the existence of a more general, integrative and mass-independent functional syndrome linking response to effect syndromes. We finally predicted that differences in response syndrome composition of hypothetical populations led to differences in ecosystem functioning.

Our results demonstrated that the ecological effects of intraspecific variability at higher levels of biological organisation were rooted in the covariations between response and effect traits. Therefore, the functional syndrome may represent an underappreciated link between genetic and environmental factors acting on individuals (Torres-Dowdall *et al.*, 2012) and the consequences of individuals on their environment (Violle *et al.*, 2007). This confirms the essential role of functional traits in eco-evolutionary dynamics (Leal, *et al.*, 2016), where variations in response traits are the basis for organisms to evolve when facing environmental variability and where the subsequent covariation with effect traits can influence environmental conditions (Figure 1). Consequently, the functional syndrome should provide novel insights into eco-evolutionary studies and could therefore represent a new linkage between ecosystem and evolutionary ecology (Matthews *et al.*, 2014). To test for the existence of a functional syndrome and fully embrace the importance of phenotypic variability for ecosystems, we suggest using a multi-trait and multi-step approach. First, we recommend measuring several phenotypic traits on each individual and explicitly discriminating response and effect trait when designing individual phenotypic studies. Second, associations among response traits (response syndrome) and effects traits (effect syndrome) should be tested independently. Third, linkage between the two aforementioned syndromes should be tested. While the repeatability of traits involved can inform on the stability of impacts of intraspecific trait variability on ecosystem functioning, we suggest that functional syndromes may result from correlations among traits arising from both intra-individual and inter-individual covariations of traits (Brommer, 2013; Brommer & Class, 2017) and might therefore not require the repeatability of all traits involved in the syndrome. The functional syndrome may further vary with the environmental contexts, due to selective pressures and plastic changes, even if its structure in a given context is still crucial for ecosystem functioning. Quantifying the temporal consistency and environmental dependency of the functional syndrome should provide an integrative understanding of the ecosystemic importance of phenotypic variability.

Our response syndrome suggested that some individuals grew more, had higher energy investment in costly organs such as chelae and were less anxious. This syndrome was correlated with trophic traits such as voracity and leaf consumption and to non-trophic traits such as the rates of nitrogen excretion and egestion. This is not surprising since growth rate and energy investment in chelae are likely linked to 'trophic traits' such as leaf consumption rate and to 'physiologic traits' such as egestion rate. Importantly, we found that the functional syndrome was partially body mass-independent. Several intrinsic linkages (e.g. hormonal or physiological) exist between individual traits (Ketterson, Atwell, & McGlothlin, 2009). The covariation between response and effect traits could for instance be driven by metabolism (Biro & Stamps, 2008; Burton *et al.*, 2011). Indeed, metabolism can vary among individuals with similar body mass (Careau *et al.*, 2008) and this variation can in turn impact effect traits. Response trait syndrome was also associated to egestion and excretion rates which are end-products of catabolism (i.e. metabolic waste) (Freire *et al.*, 2008). Therefore, integrating metabolism (e.g. standard metabolic rate) in the functional syndrome might provide new mechanistic insights into the linkages among functional traits. Almost all traits involved in the functional syndrome were significantly repeatable at a level near the 0.34 average value reported in the literature for behavioural traits (Bell, Hankison, & Laskowski, 2009). Conversely to previous observations (Biro, Adriaenssens, & Sampson, 2014), we found that growth rate was not repeatable. Growth patterns are strongly affected by the timing of moulting in crayfish, which was not recorded in the present study. However, as individuals got older, moulting became more asynchronous and less frequent. Since growth rate was measured at intervals that were independent of moulting, it likely explains the absence of repeatability in growth rate. Individuals displayed consistent behavioural and physiological states, which may explain the temporal consistency of effect traits because of their interconnections. Importantly, we confirmed that effect traits could be repeatable over a relatively long period of crayfish lifetime (here 71 days, e.g. Biro *et al.*, 2014), indicating that the effects of phenotypic variability on ecosystem functioning could be stable throughout individual life.

Our multi-trait approach suggested that response traits variability could impact several key ecosystem processes through correlation with effect traits [e.g. excretion rate affecting primary productivity and nutrient cycling (Schmitz *et al.*, 2010), consumption and egestion rates acting on decomposition rate and detritus dynamics (Gessner *et al.*, 1999)]. In addition, our modelling approach predicted impacts on litter stock dynamics and population biomass depending upon the composition in response traits of hypothetical populations. These impacts were similar to those induced by large changes in population size. This is particularly relevant in the context of biological invasions because invasive populations can display strongly phenotypically-biased populations (Juette, Cucherousset, & Cote, 2014). In addition, many natural (e.g. temperature, Biro, Beckmann, & Stamps, 2010) and human-induced [e.g. biological invasions (Zavorka *et al.*, 2017), pollution (Brodin *et al.*, 2013)] changes have been reported to alter the phenotypic structure of wild populations. Our knowledge on the distribution of phenotypic biases observed in the wild along gradients of environmental conditions is limited, and quantifying how functional syndromes vary across populations is clearly needed to quantify the ecosystem consequences of intraspecific variability. Nevertheless, changes in litter decomposition dynamics could ultimately have strong direct and indirect implications on invertebrates community (Pope, Gordon, & Kaushik, 1999), elemental cycling (release of dissolved organic and inorganic carbon, Schmitz *et al.*, 2014), food web dynamics and the phenology of ecosystem functioning (Alp *et al.*, 2016).

In conclusion, our findings support the claim that, in community and ecosystem ecology, individuals should not be considered as functionally identical (Bolnick *et al.*, 2011; Violle *et al.*, 2012). Because trait variability among individuals was structured and stable, we suggested the existence of a functional syndrome that we defined as the covariation between functional response traits and functional effect traits. Interesting perspectives would be to test the variability of this syndrome among populations. Indeed, as correlations among traits are context-dependent (Bell & Sih, 2007; Zavorka *et al.*, 2015), determining how the local conditions (e.g. density, prey abundance or abiotic factors) modulate the functional syndrome is needed. It would also be of interest to assess how it is affected by species characteristics as this may modulate specific eco-evolutionary dynamics.

Acknowledgements

We are grateful to the gravière team and our numerous colleagues for their help. We also thank Robby Stoks and two anonymous reviewers for their constructive and useful comments on a previous version of the manuscript. Crayfish collection and transport was performed under the authorisation 'Arrête Préfectoral 08-04-2014'. Financial support was provided by ONEMA (projects ISOLAC and ERADINVA) and by an 'ERG Marie Curie' grant (PERG08-GA-2010-276969).

Data accessibility: *Data from trait measurements are available at Dryad http://dx.doi.org/10.5061/dryad.rm230.*

References

ALCORLO, P., GEIGER, W. & OTERO, M. (2004) Feeding preferences and food selection of the red swamp crayfish, Procambarus Clarkii, in habitats differing in food item diversity. *Crustaceana* **77**, 435–453.

ALP, M., CUCHEROUSSET, J., BUORO, M. & LECERF, A. (2016) Phenological response of a key ecosystem function to biological invasion. *Ecology Letters* **19**, 519–527.

BASSAR, R.D., MARSHALL, M.C., LOPEZ-SEPULCRE, A., ZANDONA, E., AUER, S.K., TRAVIS, J., PRINGLE, C.M., FLECKER, A.S., THOMAS, S.A., FRASER, D.F. & REZNICK, D.N. (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences* **107**, 3616–3621.

BATES, D., MAECHLER, M, BOLKER, B & WALKER, S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

BELL, A.M., HANKISON, S.J. & LASKOWSKI, K.L. (2009) The repeatability of behaviour: a meta-analysis. *Animal Behaviour* **77**, 771–783.

BELL, A.M. & SIH, A. (2007) Exposure to predation generates personality in threespined sticklebacks (Gasterosteus aculeatus). *Ecology Letters* **10**, 828–834.

BIRO, P.A., ADRIAENSSENS, B. & SAMPSON, P. (2014) Individual and sex-specific differences in intrinsic growth rate covary with consistent individual differences in behaviour. *Journal of Animal Ecology* **83**, 1186–1195.

BIRO, P.A., BECKMANN, C. & STAMPS, J.A. (2010) Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences* **277**, 71–77.

BIRO, P.A. & DINGEMANSE, N.J. (2009) Sampling bias resulting from animal personality. *Trends in Ecology & Evolution* **24**, 63–66.

BIRO, P.A. & STAMPS, J.A. (2008) Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution* **23**, 361–368.

BOLNICK, D.I., AMARASEKARE, P., ARAÚJO, M.S., BÜRGER, R., LEVINE, J.M., NOVAK, M., RUDOLF, V.H., SCHREIBER, S.J. & URBAN, M.C. (2011) Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution* **26**, 183–192.

BOLNICK, D.I., SVANBÄCK, R., FORDYCE, J.A., YANG, L.H., DAVIS, J.M., HULSEY, C.D. & FORISTER, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**, 1–28.

BRODIN, T., FICK, J., JONSSON, M. & KLAMINDER, J. (2013) Dilute concentrations of a psychiatric drug alter behavior of fish from natural populations. *Science* **339**, 814–815.

BROMMER, J.E. (2013) On between-individual and residual (co)variances in the study of animal personality: are you willing to take the "individual gambit"? *Behavioral Ecology and Sociobiology* **67**, 1027–1032.

BROMMER, J.E. & CLASS, B. (2017) Phenotypic correlations capture between-individual correlations underlying behavioral syndromes. *Behavioral Ecology and Sociobiology* **71**.

BROWN, J.H., GILLOOLY, J.F., ALLEN, A.P., SAVAGE, V.M. & WEST, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

BUBB, D.H., LUCAS, M.C., THOM, T.J. & RYCROFT, P. (2002) The potential use of PIT telemetry for identifying and tracking crayfish in their natural environment. *Hydrobiologia* **483**, 225–230.

BURTON, T., KILLEN, S.S., ARMSTRONG, J.D. & METCALFE, N.B. (2011) What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B: Biological Sciences* **278**, 3465–3473.

CAPPS, K.A. & FLECKER, A.S. (2013) Invasive aquarium fish transform ecosystem nutrient dynamics. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20131520.

CAREAU, V., THOMAS, D., HUMPHRIES, M.M. & RÉALE, D. (2008) Energy metabolism and animal personality. *Oikos* **117**, 641–653.

CHESSEL, D., DUFOUR, A.B. & DRAY, S. (2007) ade4: Analysis of ecological data: exploratory and euclidean methods in multivariate data analysis and graphical display. R package version, 1–4.

CLAVERIE, T. & SMITH, I.P. (2007) Functional significance of an unusual chela dimorphism in a marine decapod: specialization as a weapon? *Proceedings of the Royal Society B: Biological Sciences* **274**, 3033–3038.

CORREIA, A.M. (2003) Food choice by the introduced crayfish Procambarus clarkii. *Annales Zoologici Fennici* **40**, 517–528.

COTE, J., FOGARTY, S., WEINERSMITH, K., BRODIN, T. & SIH, A. (2010) Personality traits and dispersal tendency in the invasive mosquitofish (Gambusia affinis). *Proceedings of the Royal Society B: Biological Sciences* **277**, 1571–1579.

DÍAZ, S., PURVIS, A., CORNELISSEN, J.H.C., MACE, G.M., DONOGHUE, M.J., EWERS, R.M., JORDANO, P. & PEARSE, W.D. (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3**, 2958–2975.

EL-SABAAWI, R.W., BASSAR, R.D., RAKOWSKI, C., MARSHALL, M.C., BRYAN, B.L., THOMAS, S.N., PRINGLE, C., REZNICK, D.N. & FLECKER, A.S. (2015a) Intraspecific phenotypic differences in fish affect ecosystem processes as much as bottom-up factors. *Oikos* **124**, 1181–1191.

EL-SABAAWI, R.W., MARSHALL, M.C., BASSAR, R.D., LÓPEZ-SEPULCRE, A., PALKOVACS, E.P. & DALTON, C. (2015b) Assessing the effects of guppy life history evolution on nutrient recycling: from experiments to the field. *Freshwater Biology* **60**, 590–601.

FOSSAT, P., BACQUE-CAZENAVE, J., DE DEURWAERDERE, P., DELBECQUE, J.-P. & CATTAERT, D. (2014) Anxiety-like behavior in crayfish is controlled by serotonin. *Science* **344**, 1293–1297.

FREIRE, C.A., ONKEN, H. & MCNAMARA, J.C. (2008) A structure–function analysis of ion transport in crustacean gills and excretory organs. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **151**, 272–304.

FRYXELL, D.C., ARNETT, H.A., APGAR, T.M., KINNISON, M.T. & PALKOVACS, E.P. (2015) Sex ratio variation shapes the ecological effects of a globally introduced freshwater fish. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20151970.

GESSNER, M.O., CHAUVET, E. & DOBSON, M. (1999) A perspective on leaf litter breakdown in streams. *Oikos* **85**, 377–384.

GHERARDI, F. (2006) Crayfish invading Europe: the case study of *Procambarus clarkii*. *Marine and Freshwater Behaviour and Physiology* **39**, 175–191.

HARMON, L.J., MATTHEWS, B., DES ROCHES, S., CHASE, J.M., SHURIN, J.B. & SCHLUTER, D. (2009) Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* **458**, 1167–1170.

HENDRY, A.P. (2016) *Eco-evolutionary dynamics*Princeton University Press.

HENSELER, J., DIJKSTRA, T.K., SARSTEDT, M., RINGLE, C.M., DIAMANTOPOULOS, A., STRAUB, D.W., KETCHEN, D.J., HAIR, J.F., HULT, G.T.M. & CALANTONE, R.J. (2014) Common beliefs and reality about PLS: comments on Rönkkö and Evermann (2013). *Organizational Research Methods* **17**, 182–209.

JUETTE, T., CUCHEROUSSET, J. & COTE, J. (2014) Animal personality and the ecological impacts of freshwater non-native species. *Current Zoology* **60**, 417–427.

KETTERSON, E.D., ATWELL, J.W. & MCGLOTHLIN, J.W. (2009) Phenotypic integration and independence: Hormones, performance, and response to environmental change. *Integrative and Comparative Biology* **49**, 365–379.

LARSON, E.R., ABBOTT, C.L., USIO, N., AZUMA, N., WOOD, K.A., HERBORG, L.-M. & OLDEN, J.D. (2012) The signal crayfish is not a single species: cryptic diversity and invasions in the Pacific Northwest range of Pacifastacus leniusculus. *Freshwater Biology* **57**, 1823–1838.

LEAL, M.C., SEEHAUSEN, O. & MATTHEWS, B. (2016) The ecology and evolution of stoichiometric phenotypes. *Trends in Ecology & Evolution*.

LECERF, A., DOBSON, M., DANG, C.K. & CHAUVET, E. (2005) Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia* **146**, 432–442.

MATTHEWS, B., DE MEESTER, L., JONES, C.G., IBELINGS, B.W., BOUMA, T.J., NUUTINEN, V., DE KOPPEL, J. VAN & ODLING-SMEE, J. (2014) Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs* **84**, 245–263.

NAKAGAWA, S. & SCHIELZETH, H. (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews* **85**, 935–956.

ODLING-SMEE, J., LALAND, K.N. & FELDMAN, M.W. (2003) *Niche construction the neglected process in evolution*Princeton University Press. Princeton, NJ.

PELLETIER, F., GARANT, D. & HENDRY, A.P. (2009) Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1483–1489.

PINTOR, L.M., SIH, A. & BAUER, M.L. (2008) Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. *Oikos* **117**, 1629–1636.

POPE, R.J., GORDON, A.M. & KAUSHIK, N.K. (1999) Leaf litter colonization by invertebrates in the littoral zone of a small oligotrophic lake. *Hydrobiologia* **392**, 99–112.

R CORE TEAM (2013) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

REALE, D., GARANT, D., HUMPHRIES, M.M., BERGERON, P., CAREAU, V. & MONTIGLIO, P.-O. (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 4051–4063.

ROFF, D.A. (1992) *The evolution of life histories. Theory and analysis*. New York, NY: Chapman & Hall.

ROHLF, F.J. (2005) TpsDig [programm]. *Stony Brook, NY: Department of Ecology and Evolution, State University of New-York at Stony Brook.*

ROYAUTÉ, R. & PRUITT, J.N. (2015) Varying predator personalities generates contrasting prey communities in an agroecosystem. *Ecology* **96**, 2902–2911.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013a) Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology* **94**, 1046–1056.

RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013b) Population structure determines functional differences among species and ecosystem processes. *Nature Communications* **4**.

SANCHEZ, G. (2013) *PLS path modelling with R*Trowchez Editions. Berkeley.

SCHMITZ, O.J., HAWLENA, D. & TRUSSELL, G.C. (2010) Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13**, 1199–1209.

SCHMITZ, O.J., RAYMOND, P.A., ESTES, J.A., KURZ, W.A., HOLTGRIEVE, G.W., RITCHIE, M.E., SCHINDLER, D.E., SPIVAK, A.C., WILSON, R.W., BRADFORD, M.A., CHRISTENSEN, V., DEEGAN, L., SMETACEK, V., VANNI, M.J. & WILMERS, C.C. (2014) Animating the carbon cycle. *Ecosystems* **17**, 344–359.

SIH, A., BELL, A. & JOHNSON, J.C. (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**, 372–378.

STEIN, R.A. (1976) Sexual dimorphism in crayfish chelae: functional significance linked to reproductive activities. *Revue Canadienne de Zoologie* **54**, 220–227.

TORRES-DOWDALL, J., HANDELSMAN, C.A., REZNICK, D.N. & GHALAMBOR, C.K. (2012) Local adaptation and the evolution of phenotypic plasticity in trinidian guppies (Poecilia reticulata). *Evolution* **66**, 3432–3443.

TWARDOCHLEB, L.A., OLDEN, J.D. & LARSON, E.R. (2013) A global meta-analysis of the ecological impacts of non-native crayfish. *Freshwater Science* **32**, 1367–1382.

VANNI, M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* **33**, 341–370.

VILLÉGER, S., GRENOUILLET, G., SUC, V. & BROSSE, S. (2012) Intra- and interspecific differences in nutrient recycling by European freshwater fish. *Freshwater Biology* **57**, 2330–2341.

VIOLLE, C., ENQUIST, B.J., MCGILL, B.J., JIANG, L., ALBERT, C.H., HULSHOF, C., JUNG, V. & MESSIER, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* **27**, 244–252.

VIOLLE, C., NAVAS, M.-L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. & GARNIER, E. (2007) Let the concept of trait be functional! *Oikos* **116**, 882–892.

WOOSTER, D. & SIH, A. (1995) A review of the drift and activity responses of stream prey to predator presence. *Oikos* **73**, 3.

WOTTON, R.S. & MALMQVIST, B. (2001) Feces in aquatic ecosystems. *BioScience* **51**, 537–544.

ZAVORKA, L., ALDVEN, D., NASLUND, J., HOJESJO, J. & JOHNSSON, J.I. (2015) Linking lab activity with growth and movement in the wild: explaining pace-of-life in a trout stream. *Behavioral Ecology* **26**, 877–884.

ZAVORKA, L., KOECK, B., CUCHEROUSSET, J., BRIJS, J., JOACIM NÄSLUND, ALDVÉN, D., HÖJESJÖ, J., FLEMING, I.A. & JOHNSSON, J.I. (2017) Co-existence with non-native brook trout breaks down the integration of phenotypic traits in brown trout parr. *Functional Ecology* **31**, 1582–1591.

ZHANG, D., HUI, D., LUO, Y. & ZHOU, G. (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology* **1**, 85–93.

Supplementary information for ANNEXE 1.

Supplementary material

Animal rearing and experimental design

On June 6th 2014, 240 juveniles of red-swamp crayfish (carapace length (CL), range: 20.95 mm – 35.14 mm) were collected from a single population (Lake Lamartine, south-western France, 43°30'21.5"N, 1°20'32.7"E). To avoid any behavioural bias caused by the sampling method [1], individuals were captured from different habitats using several active and passive methods. These included hand netting during the day along the shore, light trapping during the night in the limnetic habitat and baited minnow traps in the limnetic and littoral habitats over day and night. Individuals were transported to the laboratory and maintained in 50-L tanks (n = 64 tanks, 50 x 30 x 35 cm, 5 individuals per tank at the beginning of the experiment) filled with dechlorinated tap water until August 2014. Each tank was equipped with a filtering and oxygenating pump. Eight tanks were installed in each shelf (8 shelves in total) located in an air-conditioned room. Temperature was maintained at 19°C and a 12:12h light-dark photoperiod was set. On a regular basis (once a month), one-third of the water was renewed and the pumps cleaned. All individuals were fed with the same quantity of pelletized fish food 3 times per week. Moulting was not recorded because individuals were observed to consume their own exuviates, potentially leading to an underestimation of moulting rates. On June 16th 2014, crayfish were individually marked using PIT (Passive Integrated Transponder) tags (8 × 1.4 mm, FDX-B 'skinny' PIT tag, Oregon RFID, USA) inserted at the basis of the fifth pereiopods pair through an incision made with a sterile scalpel [2]. No direct mortality caused by tagging was observed in the days following tagging.

We selected a subset of 64 individuals spanning the widest possible range of boldness levels estimated over all tested crayfish in July. We classified individuals in three behavioural categories and randomly picked 20 individuals in each category (and 2 extra ones in the extreme categories). There were approximately equal numbers of males (30) and females (34) of similar sizes (mean CL = 29.9 mm). Neither CL nor body mass differed significantly between selected and unselected individuals (Wilcoxon, df = 238; CL: W = 6323, p = 0.146, and body mass: W = 6124, p = 0.301). The selected crayfish were maintained in tanks for 289 days. A total of 10 individuals died over this period of time. Two crayfish that died shortly after the beginning of the experiment were replaced by new individuals of the same sex and boldness level. These two individuals did not undergo the first feeding trial and the first and second excretion tests. Finally, an individual that lost its chelae during moulting was removed from the dataset.

Since red-swamp crayfish is legally classified as an invasive species in France, individual capture, transportation and subsequent experiments were performed under the "Arrêté Préfectoral 8 Avril 2014" from the "Direction Département des Territoires - Prefecture de Haute-Garonne". Following legislation requirements, all individuals were euthanized at the end of the experiments.

Modelling the consequences on ecosystem functioning

A mass-balance bioenergetic model was used to assess the impact of the association between the response traits syndrome and effect traits. Especially we focused on the leaves consumption rate as it can act on decomposition, a key ecosystem function of freshwater ecosystems [3,4]. Also, as the consumption could drive the population biomass, the final biomass could change across scenarios of response traits values. We specifically modelled the litter consumption rate of sub-adult crayfish because *i*) they preferentially consume detritus [5] and *ii*) they allocate all their energy toward somatic growth, as opposed to adults that would allocate some of their energy to maturation and the production of gonads.

Specifically, we used the bioenergetic model developed by [6] that has already been used with crayfish [7] to calculate the quantity of leaves consumed at time *t* by individual *i* as:

$$\text{(eq. 1) } C_{it} = Cmax_{it}.p_i.f(T)_t$$

where C is the mass-specific consumption rate (g.g^{-1}.d^{-1}), $Cmax$ is the maximum consumption rate (g.g^{-1}.d^{-1}) and a function of mass (W, Table S1), p_i is an individual proportion of $Cmax$ consumed and f(T) is a temperature dependence function (see details in Table S1). We determined the daily growth rate of individuals using an energetic mass balance equation: $C_{it} = G_{it} + M_{it} + Wa_{it}$, where M and Wa are the energy loss from metabolism and waste (g.g^{-1}.d^{-1}), respectively, and G is the somatic growth rate (g.g^{-1}.d^{-1}) (Table S1). We calculated G at time t as: $G_{it} = C_{it} - (M_{it} + Wa_{it})$, and determined the mass at t_{+1} (by adding the gain of mass, i.e. the growth rate) and the consumption at t_{+1} with the novel mass.

Intraspecific variability was assumed to influence the consumption formula (eq. 1) by modulating the p parameter. We fitted a linear regression to estimate the effect of changes in response traits syndrome (the latent variable on response traits) on the mean observed consumption rate of individuals among the three measurements performed experimentally. We used the following formula:

$$\text{(eq. 2) } C_{it} = Cmax_{it}.pi.f(T)_t + \varepsilon_i \text{ and } logit\ (pi) = \alpha.RS_i + \beta$$

where $logit(p) = log\,[\frac{p}{1-p}]$ is the so-called logit link function, RS_i is the value of the individual i on the latent variable 'response syndrome', α is the regression parameter revealing the effect of the response traits syndrome on observed consumption rate, β is the intercept of this relation, and ε is the residual error for which a normal distribution with a mean of 0 was assumed and standard deviation σ_{res} was estimated. We obtained the posterior distribution of unknown parameters (i.e. α, β and σ) using a Bayesian framework and Monte-Carlo Markov chain (MCMC) sampling, available in Jags software that we called with the *rjags* package [8] in R. We assigned non-informative priors to our three parameters: i) α and β were assumed to be normally distributed with a mean of 0 and a variance of 1000 and ii) σ was assigned to a uniform distribution limited by 0 and 10. We ran 3 parallels MCMC on 25000 iterations with a burn-in of 5000. We then tested the convergence of the MCMC by means of the Brooks-Gelman-Rubin diagnostic [9]. Model diagnostics were performed using posterior predictive p-value, and the significance of α was tested by evaluating the proportion of positive posterior values of α.

To predict the consequences of populations with different response traits syndrome values and with different densities, we first substituted the original consumption formula (eq. 1) by a modified formula (eq. 2) in the bioenergetic model. We performed the simulations for a sequence of 11 populations with divergent response traits syndrome. The values for each population were randomly sampled in the ten quantiles of the distribution observed among the 47 individuals. Also, we added one population composed of individuals with random response traits syndrome values as a control. Each population was modelled with 11 densities from 1000 to 2000 individuals with increments of 100 individuals. Individual consumptions were summed to scale up from individual to population level. To account for uncertainty, each scenario was simulated 100 times based on randomly chosen 100 MCMC subsamples (i.e. corresponding to 100 posterior values of α and β).

To estimate litter stock, calculate decomposition rate and crayfish biomass, we used parameters based on a realistic ecosystem where the experimental individuals originated from (Lake Lamartine). Firstly, daily water temperatures were sourced and averaged across seven lakes located in the area and measured in 2014 [4]. Then, assuming an average input of terrestrial litter to the lake of 1 $g.m^{-2}.d^{-1}$ (based on [10]) and that leaves primarily fell within the first 10 m along the shore (6494 m^2) during one month, the estimated litter stock was 195 kg. This litter stock allow us to assess a decomposition rate as the k using the following formula [11]:

$$\text{(eq. 3) } y = e^{-k.t}$$

where y is the percentage of mass remaining, and t the time elapsed in year. The mass of leaves remaining was obtained by deducting the population leaves consumption to the litter stock. We started the simulations from December and run the model until November of the next year to follow natural cycle. We then calculated k for 360 days from December to November. The final biomass of each simulated population was recorded. Also, to determine whether populations with divergent response traits values led to different level of invasion, we compared their biomass to the biomass of the control population.

All statistical analyses were performed using R software [12] unless specified otherwise.

Model diagnostic

The Gelman and Rubin's convergence diagnostic reached the value 1 for all parameters (i.e. α, β and σ), indicating that chains have stabilized, and have likely reached the target distribution. The median value of α was 0.187 (95% confidence interval: CI = [0.029; 0.336]), and with 98.8% of positive value indicating that α should be considered as positive. The intercept, β displayed a median of -3.287 (CI = [-3.499; -3.105]). The standard deviation σ of the residuals error had a median value of 0.003 (CI = [0.002; 0.004]). The good predicting capacities of this model were confirmed by a posterior predictive p-value of 0.53. This indicated that the model can be used to predict the consequences of the association between response traits syndrome and effect traits on the dynamic of litter decomposition and on the population biomass.

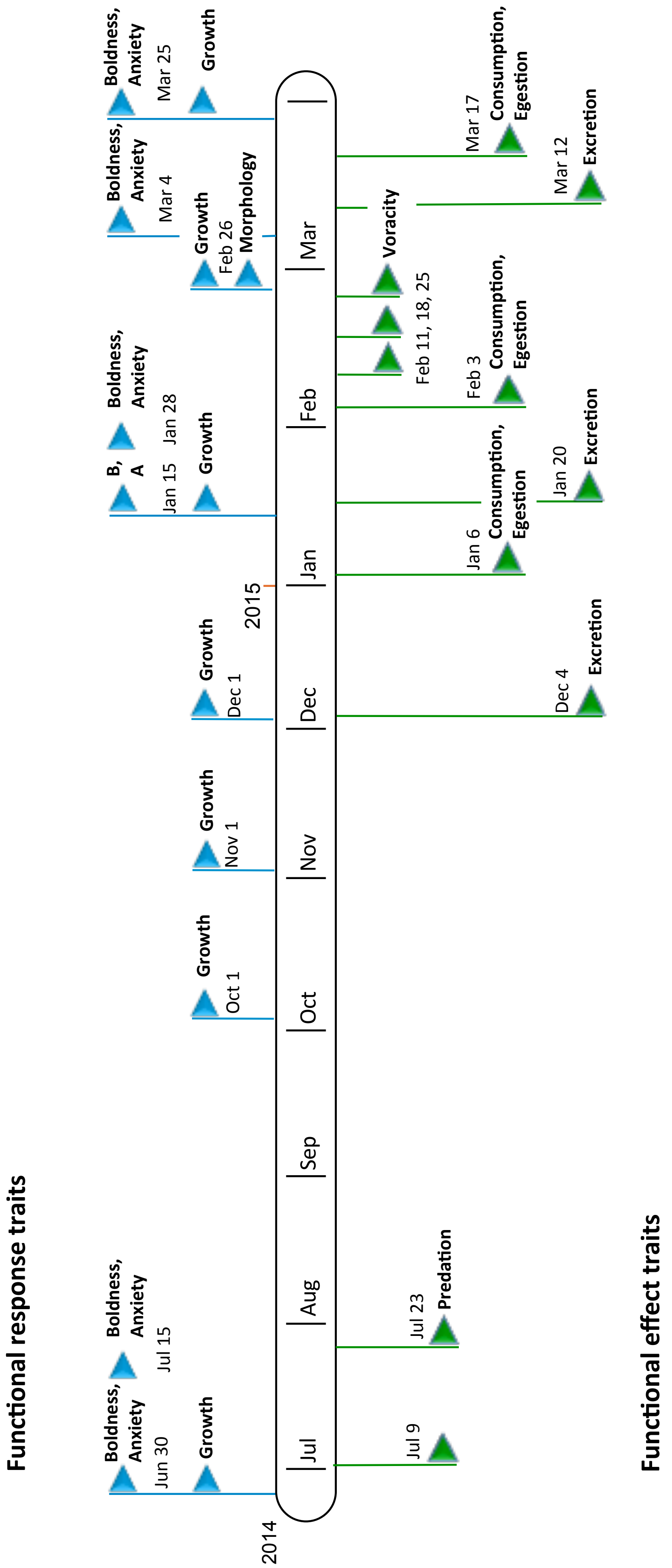

Figure S1 Time frame of the longitudinal measurements of the functional response and effect traits.

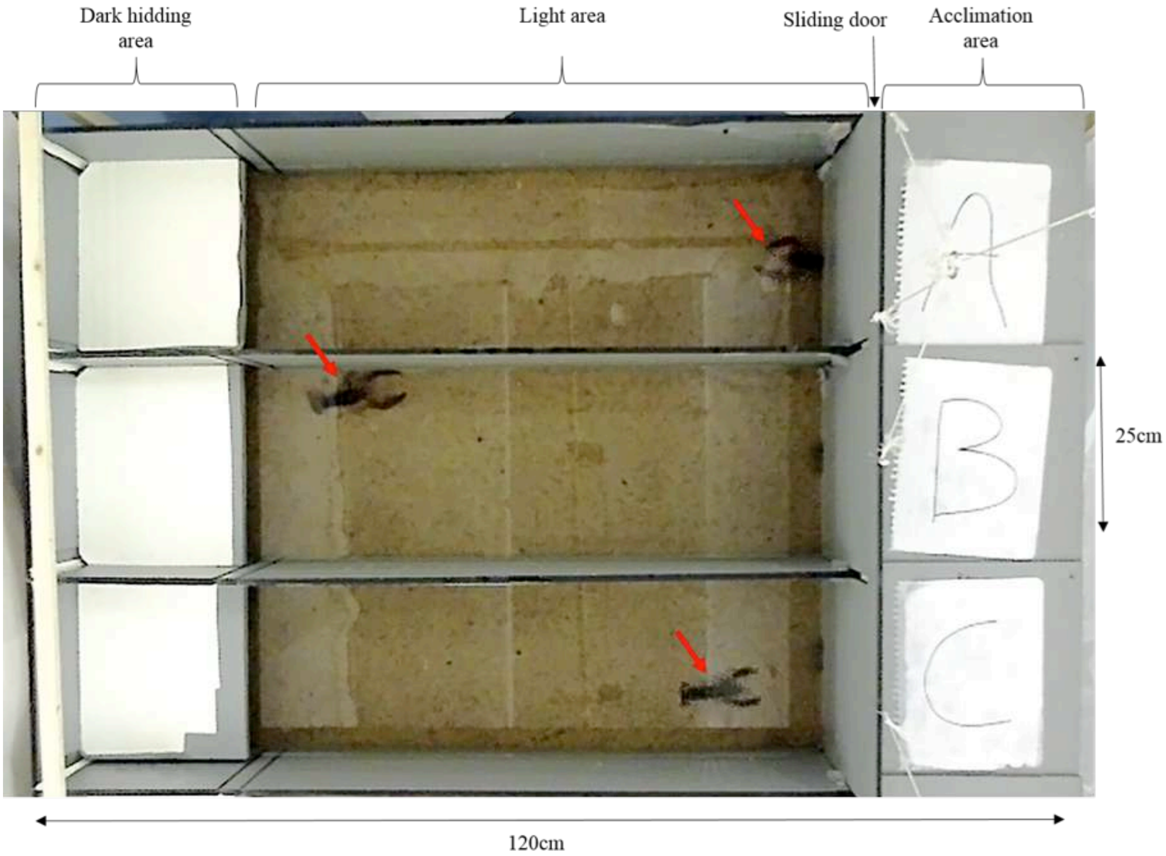

Figure S2: Three of the five experimental corridors used during behavioural assays to quantify boldness and anxiety. After the acclimation period, the sliding door was opened allowing crayfish to access the light area and dark area located at the other end of the corridor. The red arrows show individuals being assayed.

Table S1 Functional response and effect traits measured longitudinally (289 days) on individual red-swamp crayfish (*Procambarus clarkii*).

Type of traits	Category	Traits	Unit	Definition	N repetition	N individuals
Response traits	Life History	Growth rate	$\%.day^{-1}$	Somatic mass gain	6	55
	Behavioural	Boldness	s	Response to risky situation	6	55
	Physiological & Behaviroual	Anxiety	Proportion	Light avoidance and glucose secretion	6	50
	Physiological & Morphological	Chelae morphology	PCA axis	Energy allocation to costly organs and shape of chelae	1	50
Effect traits	Trophic	Consumption rate	$g.day^{-1}$	Quantity of leaves litter consumed	3	52
		Predation rate	$ind.10\ min^{-1}$	Quantity of chironomidaes predated	2	55
		Voracity	$Pellets.20min^{-1}$	Foraging behaviour and amount of food eaten	9	55
	Metabolic	Egestion rate	$g.day^{-1}$	Quantity of faeces released	3	52
		Excretion rate	$mg.L^{-1}.h^{-1}$	Quantity of ammonium excreted	3	53

Table S2 Equations used for the mass-balance bioenergetic model [6] to estimate individual consumption of red swamp crayfish (*Procambarus clarkii*). All parameters were sourced from [7], except CTO, CTM and RTM that were obtained in [13].

Function		**Formula**	**Parameter description**		**Value**
Consumption: C=Cmax.p.f(T)	Cmax	$Cmax= CA.W^{CB}$	W	Observed mass (g)	12.7 - 28.6
			CA	Consumption intercept	0.3795
			CB	Consumption coefficient	-0.2419
	f(T)	$f(T)=V^{X}.e^{(X(1-V))}$ $V=(CTM-T)/(CTM-CTO)$ $X=(Z^2.(1+(1+40/Y)^{0.5})^2)/400$ $Z=ln(CQ).(CTM-CTO)$ $Y=ln(CQ).(CTM-CTO+2)$	T	Observed temperature (°C)	5.6 - 29
			CQ	Water temperature coefficient	2.5
			CTO	Optimal temperature (°C)	23.4
			CTM	Maximum temperature (°C)	34
Metabolism: M=Respiration+ energy loss due to dynamic action	Respiration	$R=RA.W^{RB}.f(T).Act$ $f(T)=exp(RQ.T)$	RA	Respiration intercept	0.00135
			RB	Respiration coefficient	-0.4206
			RQ	Water temperature coefficient	0.0646
			RTM	Maximum temperature (°C)	34
			ACT	Activity multiplier	1
	Energy loss due to dynamic action	$S=SDA.(C-F)$	SDA	Specific dynamic action	0.18
Waste: Wa=Egestion +Excretion	Egestion	$F=FA.C$	FA	Proportion egested	0.2
	Excretion	U=UA.(C-F)	UA	Proportion excreted	0.003976

Table S3: Repeatability scores (intraclass coefficient correlation, ICC) calculated among temporal replicates. Between individual variability (BIV) and within individual variability (WIV) extracted from mixed effect linear models are also reported. Significant ICCs are reported in bold (χ^2, $p < 0.05$).

Traits	**Time interval (months)**	**Number of measurements**	**ICC**	**BIV**	**WIV**	χ^2	***p***
Boldness^R	9	6	**0.31**	5.3e-6	1.2e-5	49.49	< 0.001
Anxiety^R	9	6	**0.14**	0.0023	0.014	9.67	0.002
Voracity^R	1	9	**0.78**	14.070	3.85	114.24	< 0.001
Growth rate^R	9	6	0	0	0.104	0	1
Predation rate^E	0.5	2	**0.34**	6.02	11.71	6.86	0.0089
Consumption rate^E	3	3	**0.24**	0.008	0.026	8.11	0.0043
Egestion rate^E	3	3	**0.37**	0.0059	0.0099	19.01	< 0.001
Excretion rate^E	3	3	0	0	0.0029	0	1

Superscripts indicate the type of trait: functional response (R) and functional effect (E) traits

Table S4: Results of the Spearman correlations (rho) among response traits (boldness (n=55), anxiety (n=50), chelae morphology (n=55) and growth rate (n=55)) measured longitudinally on individual red swamp crayfish (*Procambarus clarkii*). Significant correlations ($p < 0.05$) are displayed in bold.

	Boldness	Chelae	Growth
Chelae	**0.27**		
Growth	0.014	-0.1	
Anxiety	**-0.30**	-0.002	-0.21

Table S5: Results of the Spearman correlations (rho) among effect traits (leaf consumption (n=52), egestion (n=52), N-excretion (n=53), voracity (n=55) and predation (n=55)) measured longitudinally on individual red swamp crayfish (*Procambarus clarkii*). Significant correlations ($p < 0.05$) are displayed in bold.

	Leaf consumption	Egestion	N-excretion	Predation
Egestion	**0.94**			
N-excretion	**0.38**	0.4		
Predation	0.02	0.19	0.09	
Voracity	**0.65**	**0.64**	**0.29**	0.15

References for supporting information

1. Biro, P. A. & Dingemanse, N. J. 2009 Sampling bias resulting from animal personality. *Trends Ecol. Evol.* **24**, 63–66. (doi:10.1016/j.tree.2008.10.004)
2. Bubb, D. H., Lucas, M. C., Thom, T. J. & Rycroft, P. 2002 The potential use of PIT telemetry for identifying and tracking crayfish in their natural environment. *Hydrobiologia* **483**, 225–230.
3. Gessner, M. O., Chauvet, E. & Dobson, M. 1999 A Perspective on Leaf Litter Breakdown in Streams. *Oikos* **85**, 377. (doi:10.2307/3546505)
4. Alp, M., Cucherousset, J., Buoro, M. & Lecerf, A. 2016 Phenological response of a key ecosystem function to biological invasion. *Ecol. Lett.* **19**, 519–527. (doi:10.1111/ele.12585)
5. Correia, A. M. 2003 Food choice by the introduced crayfish *Procambarus clarkii*. *Ann. Zool. Fenn.* **40**, 517–528.
6. Hanson, P. ., Johnson, T. ., Schindler, D. E. & Kitchell, J. 1997 Fish Bioenergetics 3.0.

7. Roth, B. M., Hein, C. L. & Vander Zanden, M. J. 2006 Using bioenergetics and stable isotopes to assess the trophic role of rusty crayfish (*Orconectes rusticus*) in lake littoral zones. *Can. J. Fish. Aquat. Sci.* **63**, 335–344. (doi:10.1139/f05-217)

8. Plummer, M. 2015 rjags: Bayesian Graphical Models using MCMC. R package version 3-1.

9. Brooks, S. P. & Gelman, A. 1998 General methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Stat.* **7**, 434–455.

10. Bartels, P., Cucherousset, J., Steger, K., Eklöv, P., Tranvik, L. J. & Hillebrand, H. 2012 Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* **93**, 1173–1182.

11. Zhang, D., Hui, D., Luo, Y. & Zhou, G. 2008 Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J. Plant Ecol.* **1**, 85–93. (doi:10.1093/jpe/rtn002)

12. R Core Team 2013 R: A Language and Environment for Statistical Computing.

13. Croll, S. L. & Watts, S. A. 2004 The effect of temperature on feed consumption and nutrient absorption in *Procambarus clarkii* and *Procambarus zonangulus*. *J. World Aquac. Soc.* **35**, 478–488.