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Exotic or not, leaf trait dissimilarity modulates the effect of dominant species on mixed litter decomposition

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Summary

1. It has long been recognized that leaf traits exert a crucial control on litter decomposition, a key process for nutrient cycling, and that invading species can greatly alter such soil processes via changes in mixed litter trait composition. Trait effects on ecosystem processes are hypothesized to operate via changes in either dominant trait values in the community (often calculated as community-weighted mean trait values; CWM) or trait functional diversity (dissimilarity between species trait values; FD). Few have studied the effects of these community trait components in tandem due to their interdependence.

2. We studied litter mixture decomposition using three exotic and six native European tree species with a range in litter decomposability, to disentangle the unique and combined roles of CWM and FD in explaining net litter mixture mass loss.

3. We showed that while CWM exerted the strongest effect on mass loss, FD modulated its effects, increasing mass loss in mixtures with low mean decomposability and decreasing mass loss in mixtures with high mean decomposability. Litter species identity and native/exotic status explained relatively little additional variation in mass loss after accounting for CWM and FD. We further showed that alterations to CWM and FD were more important than the replacement of a native species with an exotic counterpart in predicting mass loss.

4. *Synthesis:* Our results indicate that the effect of adding an exotic or losing a native species on litter decomposition rate can be predicted from how a species alters both CWM and FD trait values. This supports the idea that the repercussions of exotic species on ecosystem processes depends on the extent that introduced species bear novel traits or trait values and so on how functionally dissimilar a species is compared to the existing species in the community.

Key-words: biodiversity effects on ecosystems, exotic species, invasion ecology, leaf litter decay, leaf litter morphology and nutrient content, leaf litter traits, mass-ratio hypothesis, non-additive effects

Introduction

Communities world-wide are being dramatically altered by anthropogenic factors and the resulting species loss, and the introduction of non-native species has become a global concern (Sax & Gaines 2003; MEA 2005). One major concern is that invasive species might lead to ecosystem changes, but there are still many gaps in our understanding of the impact of exotic species on ecosystem functioning. Community trait composition has emerged as having a key role in driving

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many ecosystem processes, and trait-based approaches can be useful to understand and predict the effect of changes in species composition on ecosystems (Suding *et al.* 2008; Luck *et al.* 2009; Mouillot *et al.* 2011). While there is considerable debate surrounding the importance of trait dissimilarities between exotic and native species in predicting the success of invasion (Dawson, Maurel & van Kleunen 2015; Leffler *et al.* 2015), the role of such dissimilarities for predicting the potential effects of exotic species on ecosystem processes still deserves more attention (Wilsey & Polley 2006; Wardle *et al.* 2011). Understanding how trait composition determines the potential effects of species on ecosystem processes will therefore be integral to identifying the potential consequences of non-native species invasions.

In plant communities, changes in trait composition can have direct effects on ecosystem processes such as litter decomposition, for example via the afterlife effect of leaf litter traits determining resource quality and microenvironmental conditions for decomposers (de Bello *et al.* 2010; Makkonen *et al.* 2013). Recent studies have shown litter decomposition to correlate with leaf C and N content but also with other litter traits, such as calcium content, leaf tensile strength and dry matter content (e.g. Kazakou *et al.* 2006; Santiago 2007; Fortunel *et al.* 2009; Makkonen *et al.* 2012; Vos *et al.* 2013). The decay of leaf litter constitutes an important part of the nutrient cycle and is a key process in ecosystem sustainability. Several studies have looked at the impact of native and exotic species traits on litter decomposition (Ashton *et al.* 2005; Kueffer *et al.* 2008; Kurokawa, Peltzer & Wardle 2010; Halabuk & Gerhátová 2011; Castro-Díez *et al.* 2014). A meta-analysis by Liao *et al.* (2008), including 94 experimental studies, revealed that invaded ecosystems had on average 117% faster litter decomposition. This is thought to be at least partly driven by trait differences between invading and native species (Metcalfe, Fisher & Wardle 2011), and, in general, it is expected that exotic species will have a large impact on processes like decomposition of mixed-species litters when differing in traits compared to the rest of the community (Funk *et al.* 2008). Contrary to this belief, Jo, Fridley & Frank (2016) found no consistent differences in decomposition rates between natives and non-natives in a common garden experiment including 80 species, highlighting that litter decomposition rate in itself is not the pathway by which invasive species impact soil processes. This stresses the importance of challenging the assumption that invasive species affect soil processes linked to decomposition when studying the effects of non-native species on the environment (Prescott & Zukswert 2016). In particular, trait-based approaches, such as used in this study, can offer a promising tool for inferring possible effects of exotic species on soil processes (e.g. Drenovsky *et al.* 2012; Metcalfe, Fisher & Wardle 2011; Jo, Fridley & Frank 2016 and other references above).

The establishment of exotic plant species, and the potential loss or replacement of native species (and their traits) can affect two components of the community trait composition with potential consequences for litter decomposition: (i) the community-weighted mean of trait values (CWM), which is

the average of the values of a particular trait of species present in a community, weighted by relative abundances of the component species (Garnier *et al.* 2004; Ricotta & Moretti 2011) and (ii) functional diversity (FD), which reflects the variation in values of a specific trait, or sets of various traits, of species within a community and can be calculated in a number of ways (Schleuter *et al.* 2010). Agreement is growing that CWM and FD are two complementary indices to understand community functioning (Ricotta & Moretti 2011; Dias *et al.* 2013) and both have been found to explain significant variation in ecosystem processes (Laughlin 2011; Mouillot *et al.* 2011; Roscher *et al.* 2012; Bílá *et al.* 2014).

Two main hypotheses connect species traits, and particularly CWM and FD, to ecosystem processes. The mass-ratio hypothesis (Grime 1998; hereafter MRH) states that the effect of a species on a given ecosystem process is proportional to its relative abundance in the community (Garnier *et al.* 2004). If the MRH holds, then ecosystem processes should correlate strongly with CWM values of mixed-species litters, based on species-specific trait values. CWMs of leaf litter traits have been shown to be accurate predictors of nutrient cycling (Pakeman, Eastwood & Scobie 2011), and there is much support for the MRH (e.g. Quested *et al.* 2007; Mokany, Ash & Roxburgh 2008; Laughlin 2011; Bílá *et al.* 2014) in the control of leaf litter decomposition. However, in natural ecosystems, the mixture of litter of different species also creates the potential for species interactions and the occurrence of non-additive effects on litter decomposition. In fact, non-additive effects (those not predictable from the sum of the effect of single species) of litter mixing are one of the most commonly reported outcomes of litter mixing experiments (Wardle, Bonner & Nicholson 1997; Gartner & Cardon 2004; Makkonen *et al.* 2013; Vos *et al.* 2013). Tardif & Shipley (2013) proposed the 'idiosyncratic annulment' hypothesis (IAH) to explain why MRH has strong explanatory power, despite the frequent observation of non-additive litter mixing effects. According to IAH, non-additive effects are assumed to be equally likely to be positive or negative, leading the annulment of non-additive effects (on average) and preserving the relationship between CWM and decomposition. On the other hand, any deviation from the MRH (i.e. non-additive litter mixture effects) could be revealed to be the effect of trait dissimilarity between species (FD). Where FD is correlated with ecosystem processes, support is provided for the diversity hypothesis, which predicts that species traits will affect ecosystem processes via mechanisms such as facilitation among coexisting species (Tilman, Wedin & Knops 1996; Petchey, Hector & Gaston 2004; Hooper *et al.* 2005; Díaz *et al.* 2007; Mouillot *et al.* 2011). During litter decomposition, non-additive effects can be the result of transfer of nutrients or deterrent compounds (e.g. polyphenols) from leaves with higher to leaves with lower concentration of these elements (Handa *et al.* 2014), that is when a species differs in its trait values from those around it. FD has been shown to promote non-additive effects in litter decomposition (Heemsbergen *et al.* 2004); however, the effect of FD on litter decomposition has sometimes yielded contradictory results (Gartner & Cardon 2004; Hättenschwiler & Gasser 2005).

Here, we tested whether the effect of native and exotic species on leaf litter decomposition can be understood by their traits and the resultant CWM and FD of a given litter mixture. We performed a litterbag experiment encompassing a wide range of CWM and FD of traits involved in decomposition processes and containing species mixtures with and without exotic species. We used the framework proposed by Dias *et al.* (2013) to tease apart the, otherwise confounding, effects of CWM and FD. This approach allowed us to examine both how changes in community composition can affect litter decomposition and to what extent mixing native and exotic litter contributes to such effects. Given prior knowledge that the MRH is known to produce good predictions of mixed litter decomposition, we expected CWM to explain the highest proportion of litter mixture decomposition and FD to explain additional effects (Bílá *et al.* 2014). If the IAH holds, we would expect that the occurrence of positive or negative non-additive litter mixing effects might depend on the trait dissimilarity of component species, but at any given CWM, the direction of the effect is equally likely to be positive or negative. Another option is that the effect of FD on decomposition, and thus the direction of non-additive effects, will depend on the litter trait values of species present in a community (Bílá *et al.* 2014), with FD promoting positive non-additive effects on slow-decomposing mixtures and the opposite fast-decomposing mixtures (Makkonen *et al.* 2013; Bílá *et al.* 2014). We expected that the effect of species on decomposition will depend on their litter trait values, and thus their potential to alter CWM and FD, rather than specifically their native/exotic status. In other words, we expect that the effect of CWM and FD will be consistent in both mixtures of only native litter and those containing exotic species. If trait values are not a reliable predictor of litter decomposition, then both species identities and native/exotic status should considerably improve predictions compared to trait values alone. While we expect non-additive effects to be generally weaker in magnitude compared to those of litter mixtures mean quality (that is MRH), the question of their relative strength remains open. Thus, we hypothesize that non-additive effects could modulate the effects of MRH.

Materials and methods

LEAF LITTER SAMPLING AND TRAIT MEASUREMENT

Between September and November 2012, the leaf litter of 14 preselected tree species, nine native and five exotic (as defined by Mandak & Pysek 1998), was sampled from forests around the city of Bellinzona, South Switzerland (46°11′54″N, 9°1′30″E). Species were preselected to include a range of decomposition rates which can potentially coexist under natural conditions (see Table S1 in Supporting Information). Leaf litter was collected beneath two to five individual trees per species twice a week. Freshly senesced leaves were collected from the ground by hand and cleaned in the laboratory. Care was taken to avoid leaves with any obvious signs of visible damage, infection or attack by herbivores. Leaves were then air-dried in a dark, ventilated room for 5 days and stored in paper bags.

We measured four chemical traits and one physical trait recognized as drivers of leaf litter decomposition in the presence of the full decomposer food web (Enríquez, Duarte & Sand-Jensen 1993; Perez-Harguindeguy *et al.* 2000; Cornelissen *et al.* 2003; Santiago 2007): total C and N content (%), calcium (Ca) and magnesium (Mg) content (mg g^{-1}), and leaf tensile strength (N mm^{-1}). Leaf tensile strength often correlated with leaf dry matter content and lignin content, and it was chosen here as it is a good integrative measure of physical resistance to consumption by macrodetritivores (Perez-Harguindeguy *et al.* 2000). Leaf C, N and Ca content have proved to be good predictors of leaf litter decomposition (e.g. Cornelissen 1996; Kazakou *et al.* 2006; Santiago 2007; Fortunel *et al.* 2009). Mg content was included as, like Ca, it is an important element in the cuticle of macrodetritivores (Becker, Ziegler & Epple 2005). We focus on these 5 traits while being aware that other traits could also be of importance. On the other hand, a large selection of traits in general does not increase our mechanistic understanding as traits are generally correlated. Moreover, many litter mixture studies are set up in such a way that the influence of macrodetritivores, which are key organisms in litter decomposition, is excluded (for instance using litterbags with a small mesh size). In studies that do allow entrance of macrodetritivores to litter (such as in our case), it is often shown that next to the usual suspects other traits become important, such as Ca and Mg content (Vos *et al.* 2013), as these elements are important for the build-up of their exoskeleton. To measure the chemical traits, dried leaves of two composite subsamples (100 mg of dried leaves crushed into small fractions per subsample) were ground using standard procedures (Cornelissen *et al.* 2003). Leaf tensile strength was measured on seven leaves per species using an Ultratest Mecmesin AFG 1000N (Advanced Force Gauge). Species average trait values were used in all analyses.

LITTER DECOMPOSABILITY GROUPS

A principal component analysis (PCA) and a cluster analysis of the physicochemical trait values, based on Gower dissimilarity measure with Ward linkage clustering, were used to identify three groups of litter species that differ in decomposability: slow, intermediate and fast (Fig. S1; step 1 in Fig. 1). Other clustering approaches gave similar groups of litter species. Hereafter, these are referred to as 'decomposability groups'. Out of the initial 14 species, the final set of nine species were selected to give three species per decomposability group, that is high decomposability: *Prunus serotina*, *Acer pseudoplatanus* and *Fraxinus excelsior*; intermediate decomposability: *Acer platanoides*, *Castanea sativa* and *Paolownia tomentosa*; and low decomposability: *Quercus rubra*, *Fagus sylvatica* and *Quercus robur*. Among them, *P. tomentosa*, *P. serotina* and *Q. rubra* are exotic species in this region of Europe, with one exotic species in each decomposability group.

EXPERIMENTAL DESIGN

A modified version of the approach proposed by Dias *et al.* (2013) was used to create a quasi-orthogonal design regarding litter mixture CWM and FD. Such a design is needed to avoid intrinsic relationships between CWM and FD and separate their effects on litter decomposition, which will otherwise be entangled when using natural communities or random assemblages. In our design, litter species richness and mass were held constant (four species, 1g each) in all litter mixtures; therefore, CWM is equal to the simple mean of trait values of the species present in the mixture. Dominant species effects
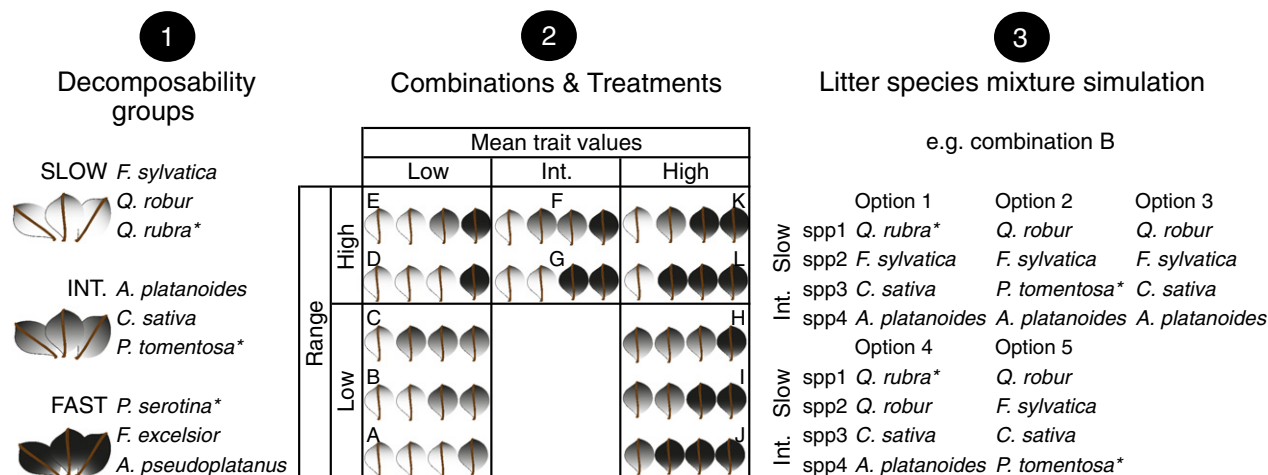
Fig. 1. Process diagram showing the simulation of litter mixtures from decomposability groups. Asterisk at the end of a species name indicates status as exotic. Step 1) Based on five key traits, we created 3 decomposability groups with expected differences in species decomposition rates. Step 2) All 12 possible combinations of these groups (labelled A-L) were formed and assigned to one of 5 'treatments', indicated by the boxes, with different mean (CWM) and range (FD) of trait values: LL, LH, IH, HL and HH. Step 3) Within each of the 12 combinations, we created all possible assemblages of species; combination B is given as an example (For more details, see main text and Appendix S1).

can therefore be interpreted, for example, as the number of species from each decomposability group present in a litter mixture.

Twelve different ways of combining the three decomposability groups were possible (see combinations A-L in step 2 of Fig. 1 and Table S2), including one slow-decomposing species, two intermediate and one fast. These combinations exhibit a range of CWM and FD values. As a first approximation, species were scored a value depending on the decomposability group they belonged to (0, 1 and 2 for slow, intermediate and fast, respectively), and the mean (CWM) and range (FD) of decomposability groups (and therefore traits) in each combination were calculated (Fig. S2). This yielded five CWM and FD 'treatments' (step 2 in Fig. 1; Table S2): LL (low CWM/low FD), LH (low CWM/high FD), IH (intermediate CWM/high FD), HL (high CWM/low FD) and HH (high CWM/high FD). As discussed by Dias *et al.* (2013), combinations with intermediate CWM and low FD are generally difficult to obtain. Analyses were also run selecting only litter mixtures from LL, LH, HL and HH treatments (Fig. S2). We also considered in our analyses other possible ways of computing CWM and FD using quantitative trait values instead of decomposability groups.

Finally, all possible litter species mixtures (here after litter mixtures) of the nine selected species were considered within each of the 12 'combinations', with the constraint that a maximum of one exotic species was present in each mixture, giving a total of 75 litter mixtures (see step 3 in Fig. 1 for an example). By considering all possible litter mixtures, we were also able to test the effect of individual species (independently of their trait values). Constraining the litter mixtures to contain only one exotic species allowed us to explore the effect of including an exotic species, and thus, the effect of its traits might have a native/exotic litter mixture.

In December 2012, litter was oven-dried at 40 °C for 2 days and placed into 18 cm × 18 cm litterbags according to the 75 simulated litter mixtures. Each species in each litterbag contributed with a dry weight of 1 g (net total of 4 g per litterbag). A fine mesh (1 mm) was used on the bottom of the litterbag to avoid the loss of litter material, with a coarser (4 mm) mesh on top to allow access of macrofauna to the litter. The experimental site for litterbag incubation was situated within a mixed forest (Magadino: 46°8′58″N, 8°54′31″E)

in southern Switzerland (250 m a.s.l.). The site was chosen as the litter layer was dominated by two tree litter species not included in the study group: *Larix decidua* and *Liriodendron tulipifera*. This was done to avoid any potential home field advantage for any studied litter species (Freschet, Aerts & Cornelissen 2012).

Litterbags were placed into the field on 31 December 2012 in five neighbouring replicate plots (3.5 m × 4 m) separated by fences. All plots received one litterbag of each of the 75 litter mixtures in a random position within the plot. In addition to the litter mixtures, litterbags filled with monocultures of each litter species and ten extra litterbags of the fastest and slowest decomposing species (*F. excelsior* and *Q. robur,* respectively). These were initially checked for litter mass loss after 4 months of incubation and then checked weekly to determine when either 50% mass of the fastest decomposing species or 10% mass of the slowest species had been lost (Cornelissen 1996). While we used five traits to infer three levels of litter decomposability, the monoculture litterbags allow us to measure directly species-specific decomposability, which is the combined result of positive and negative effects of several functional traits. The experiment was terminated and litterbags were collected from the field on 3rd June 2013 based on the criterion of 50% mass loss for the fastest decomposing species. The remaining litter was dried (40 °C, 48 h) and weighed as before to the nearest μg. Decomposition was expressed as the change in mass (g dry weight) of litter mixtures over the course of the experiment, calculated by subtracting the oven-dry weights at the end of the experimental period from those at the beginning, hereafter referred to as net litter mass loss.

COMMUNITY FUNCTIONAL INDICES

In addition to the five treatments based on the decomposability groups (see above), we computed CWM and FD of each single species' physicochemical traits as well as actual decomposition values (in monocultures, see previous section) for each of the distinct litter mixtures using the package FD (Laliberte & Shipley 2011) in R (R Core Team 2014). After calculating dissimilarity (Gower) between the nine species' traits, we computed FD of each litter mixture using the Rao quadratic entropy index (Leps *et al.* 2006; Ricotta &

Moretti 2011). As all litterbags have the same number of species, the index corresponds to the mean pairwise dissimilarity between species in a mixture. For clarity, CWM and FD values based on actual decomposition values are referred to as $CWM_{mass.loss}$ and $FD_{mass.loss}$ hereafter.

DATA ANALYSIS

All data processing and statistical analyses were carried out in R (R Core Team 2014). We used lme4 (Bates *et al.* 2014) to fit linear mixed effect models (LMMs) to our data, fitting plot as a random effect term to account for baseline variability in decomposition between the five replicate plots. The specific designs of models used to answer each question are described in detail below. Litter mass loss in each litterbag was the response variable for our models unless otherwise stated. Given that the initial mass of each litterbag was the same, similar results are obtained when expressing decomposition as percentage in mass loss.

ANALYSIS 1: ROLE OF CWM AND FD IN LITTER DECOMPOSITION

In order to test the role of CWM and FD in litter decomposition, we used two alternative approaches. First we fitted a model with CWM and FD treatment as a factor with five levels (LL, LH, IH, HL and HH, respectively) corresponding to the five treatments shown in Fig. 1, step 2. Here, the statistical interest lies in the potential differences between the five treatment levels (notice that using four levels, without considering IH, Fig. S3, led to the same results). Tukey contrasts for multiple comparisons, calculated using the package 'multcomp' (Hothorn, Bretz & Westfall 2008) with Bonferroni adjustments, were used to assess the significance of any differences in litter mass loss found. Secondly, we computed $CWM_{mass.loss}$ and $FD_{mass.loss}$ values based on species-specific decomposition (Fig. S4) for each litter mixture. The main effects of $CWM_{mass.loss}$ and $FD_{mass.loss}$ as well as the interaction term between the two were included as continuous fixed effects. Significant interaction would indicate that the effect of one was mediated by the value of the other. The $CWM_{mass.loss}$ of each litterbag is equal to the expected mass loss based on the monocultures (i.e. only additive litter mixing effects), corresponding to the MRH predictions. Thus, if either the main effect of FD or the interaction between FD and CWM is significant predictor of litter mass loss, some variation not accounted for MRH predictions is due to non-additive effects. Although it is possible to test for non-additive effects in alternative ways (see for example Loreau & Hector 2001; Vos *et al.* 2013), the approach we took makes it possible to test for an interaction between CWM and FD. We also ran additional analyses to test whether some of the other five specific traits explained additional variation in litter mass loss, compared to decomposability alone. A model was fitted with all CWM and FD scores included as potential fixed effects. As there were a high number of correlated trait values available as covariates, which could possibly confound backward selection with likelihood ratio tests (LRT) approaches, the information theoretic model selection described in Appendix S2 was used.

ANALYSIS 2: INDIVIDUAL SPECIES' EFFECTS BEYOND THEIR TRAITS

We explored the effect of the identity of single species on litter mixture mass loss beyond the effect of their measured traits. To do this, the residuals of the final models from the previous steps were fitted in a linear model, with presence/absence of the nine species as categorical predictors. Graphical inspection showed the residuals of models described above to be approximately normally distributed and no evidence of correlation of residuals within plots was found, justifying the use of linear models for these analyses. Any species that explained a significant portion of the variation would be indicative of it having an effect on mixture decomposition outside of that predicted by the measured traits.

ANALYSIS 3: IMPACT OF EXOTIC SPECIES

Different models were fitted to explore possible effects of mixing native and exotic species' leaf litter. First, we tested whether there was a difference in mass loss of litter mixtures where exotic species were present vs. absent, controlling for the fact that litterbags contained species of varying mass loss. To do this, we fitted a LMM to model the relationship between observed litter mixture mass loss and expected mass loss based on monocultures ($CWM_{mass.loss}$) and the absence or presence of exotic species as a fixed effect. Secondly, within the combinations B, E, F, G, I and K (see step 2 in Fig. 1 & Table S2), there were mixtures with and without exotic species (step 3 in Fig. 1). Within these combinations, if an exotic was present, it must have replaced a native counterpart with relatively similar trait values. By including the interaction between the categorical variable 'combination' (B, E, F, G, I and K) and one coding for exotic presence/absence, we tested the effect of replacing a native counterpart with an exotic of similar trait values (in terms of mass loss).

MODEL SELECTION

In all models (unless specified otherwise), to test the significance of terms of interest, LMMs were created by specifying the maximal model of fixed and random effects, along with any biologically relevant interactions, followed by model simplification. Sequential, backwards deletion of terms from the maximal model was performed, as is appropriate for data that cannot be fully orthogonal (Dias *et al.* 2013). To test the significance of removing a term, the explanatory power of simplified models was compared to the maximal model using LRT (Pinheiro & Bates 2000). For more details on this, see the text in Appendix S2. Information theoretic model selection (using AICc) was also performed in addition to LRT methods; however, in all cases, the final models did not differ from the LRT approach. As a measure of good fit, R^2 equivalents for mixed models representing the proportion of variance explained firstly for the fixed effects and secondly the fixed and random effects combined, marginal R^2 and conditional R^2, respectively, were obtained using the method by Nakagawa & Schielzeth (2013), implemented via the package MuMIn (Barton 2014). Outliers were identified using graphical inspection of both the raw data and model residuals leading to removal of four litterbags (widespread across the treatments) from all analyses.

Results

Mass loss of single litter species followed the pattern predicted by decomposability groups based on physicochemical litter traits. The three 'slow-decomposing' species exhibited on average the lowest mass loss, followed by 'intermediate-decomposing' species, while the 'fast-decomposing' species showed the highest mass loss (Fig. S3). There was some overlap in mass loss between species of the intermediate and

the fast decomposability group, most notable in *A. platanoides* and *P. serotina*. A mixed model indicated that decomposability groups explained 65% of variation in single species litter mass loss (Table S3).

THE ROLES OF CWM AND FD

Across all our models CWM was the main driver of mass loss in litter mixtures, causing a clear increase in net mass loss as the presence and mass of fast-decomposing species increased (Fig. 2). The effect of FD was dependent upon the CWM of the litter mixture, as shown in the combined effect of CWM and FD (Fig. 2) and by a significant interaction term between $CWM_{mass.loss}$ and $FD_{mass.loss}$ using the continuous data (-0.765 ± 0.375, Chi-sq = 4.152, d.f. 1, $P < 0.05$; Table 1). Given a starting litterbag mass of 4g, this is approximately equivalent to 19% of the total mass. Generally, at low CWM, the effect of FD was positive and the opposite was observed at high CWM (Figs 2 and 3). Regarding the CWM and FD values based on decomposability groups, increasing FD at a low CWM (LL-LH) caused an average increase of 15.6% in mass loss. Mixtures with high CWM but a low FD (HL) decomposed on average 26.5% faster than mixtures with a high CWM and FD (HH) (Fig. 2; Table S4 for model output). The fixed effects of the model explained 42% of the variance (marginal R^2). The results from the model using $CWM_{mass.loss}$ and $FD_{mass.loss}$ echoed these (Fig. 3; Table 1).

Although the possibility to include other continuous CWM and FD values (e.g. those calculated from the physicochemical traits) alongside $CWM_{mass.loss}$ and $FD_{mass.loss}$ was explored, the final models were the same as above, including $CWM_{mass.loss}$ and $FD_{mass.loss}$ only. On one run, the model was constrained to include only CWM and FD scores from the physicochemical traits; the variables selected and relative and absolute model fit descriptors (as compared with the 'best' model) are shown in Table S5. The fixed effects of the model including $CWM_{mass.loss}$ and $FD_{mass.loss}$ explained approximately 7% more of total variation in litter mass loss than one
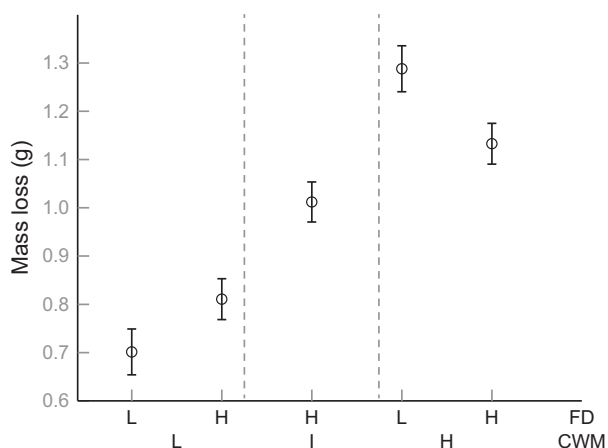
Table 1. Linear mixed-effects model to test for and quantify effects of $CWM_{mass.loss}$ and $FD_{mass.loss}$ on net mass loss of litter mixtures

	Number of observations: 362, grouping factors: Plot, 5			
	Random effects			
Plot	0.003 (10%)			
Residual	0.031 (90%)			
	Fixed effects			
	Estimate	SE	X^2 (1 d.f.)	P
Intercept	0.996	0.028		
$CWM_{mass.loss}$	0.858	0.049	222.59	***
$FD_{mass.loss}$	0.051	0.087	0.346	ns
Interaction	−0.765	0.375	4.152	*
	Marginal R^2 0.566 conditional R^2 0.609			

***$P < 0.001$; *$P < 0.05$; $^{ns}P > 0.05$. Estimated effect sizes and their standard errors are show for all fixed covariates, with significance of removal of term assessed using likelihood ratio tests (see main text). All covariates have been centred; therefore, model intercept calculated when both covariates are equal to 0 (i.e. their mean values).
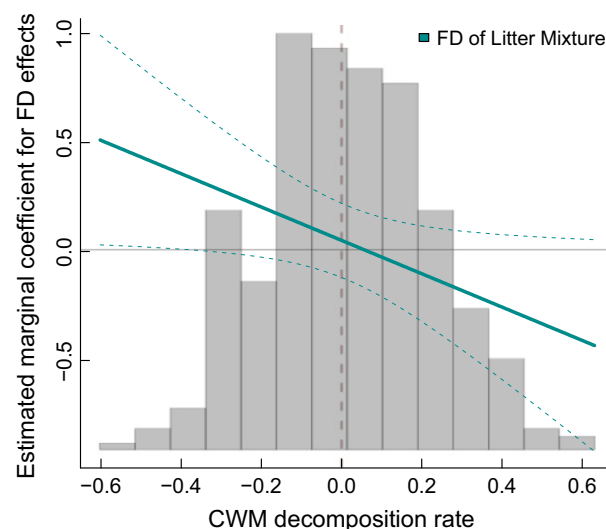

Fig. 3. Marginal effect of $FD_{mass.loss}$ on litter mixture decomposition, across a range of values of $CWM_{mass.loss}$. Histogram represents distribution of centred covariate $CWM_{mass.loss}$ with dashed red line representing the centred mean. Dashed lines show confidence interval 95% surrounding the marginal effect.

based purely on physicochemical trait values (marginal $R^2 = 0.566$ vs. 0.526, respectively).

INDIVIDUAL SPECIES' EFFECTS

The outputs of models describing the effect of specific species on residuals from CWM and FD are shown in Table S7. In the model based on decomposability groups, litter mixtures containing *A. platanoides* and *F. excelsior* decomposed faster than

Fig. 2. Mean (±SEM) litter net mass loss (see Appendix S3 for model outputs). L = low; I = intermediate; H = high. All differences between treatment means are significant ($P < 0.05$).

expected (residuals = 0.108 ± 0.020, F = 30.486, $P < 0.001$; residuals = 0.125 ± 0.020, F = 40.744, $P < 0.001$, respectively). In contrast, *C. sativa* was negatively associated with model residuals (residuals = −0.059 ± 0.020, F = 8.999, $P < 0.01$). Together, these species effects explained a relatively small part of the variation (adjusted R^2 = 0.199) in model residuals. For the model based on continuous values of $CWM_{mass.loss}$ and $FD_{mass.loss}$ (Table 1; Fig. 3), residuals were positively associated with mixtures containing *P. serotina* (residuals = 0.074 ± 0.022, F = 11.61, $P < 0.001$) and *Q. rubra* (residuals = 0.046, F = 4.45 ± 0.022, $P < 0.05$). Although the inclusion of these species was found to be statistically significant, the additional explained variation was very low (adjusted R^2 = 0.028), indicating that the effect of these species, other than via their traits, was very small.

THE EFFECT OF EXOTIC SPECIES

There was no evidence that the presence of an exotic litter species in the litter mixture had any significant effect on net litter mass loss or led to non-additive effects (Table C6a). There was also no evidence to support that there was any impact of replacing a native counterpart with an exotic species on net mass loss, as examined within the relevant combinations (B, E, F, G, I and K; Table C6b) as again neither the inclusion of the interaction term between combination and the presence or absence of exotic species nor the main effect of exotic presence/absence improved the explanatory power of the model.

Discussion

Leaf litter mass loss was greatly affected by CWM trait values, lending further support to the mass-ratio hypothesis, that is the predominance of litter quality of the most abundant species, as a driver of mixed-species litter decomposition, (Grime 1998; Laughlin 2011; Bílá *et al.* 2014). Our results also confirm the expectation that FD of mixed-species litter could help to explain biodiversity influences on ecosystem processes beyond mass-ratio effects (Heemsbergen *et al.* 2004; Meier & Bowman 2008; Lecerf *et al.* 2011; Coulis *et al.* 2015). Although the main effect of FD was generally weak, we showed an important interaction between FD and CWM in explaining mixed-species litter decomposition. Thus, FD modulates the effect of CWM by increasing decomposition in communities dominated by species with low decomposability, while decreasing decomposition in communities with higher decomposability (see Figs 2 & 3 and significant interaction between $CWM_{mass.loss}$ and $FD_{mass.loss}$).

In mixtures with low decomposability, the majority of the litter is slow decomposing and therefore the inclusion of species with different traits, for example a high N content might promote nutrient transfer (Handa *et al.* 2014) or improve the microenvironmental conditions (Cornelissen 1996; Hector *et al.* 2000; Makkonen *et al.* 2012). At the other extreme, in mixtures with high decomposability, most species are fast decomposers and thus adding species that increase FD is likely

to create the opposite effect, possibly creating a litter mixture that is less appealing to detritivores due to dilution of essential nutrients and increasing the content of more recalcitrant compounds. Where this impacts surrounding species, the effect on litter mixture decomposition seen by changing FD will diverge from that expected by the purely the alteration of the average value (CWM) alone. Additionally, the change in direction of the effects of FD on litter decomposition depending on the CWM of the mixture refutes the predictions of the idiosyncratic annulment hypothesis (Tardif & Shipley 2013), showing that positive and negative non-additive effects are not equally likely to occur everywhere (i.e. they were non-random in relation to CWM). These results further offer insight into why experiments studying the effect of FD on ecosystem processes may yield contradictory results (Gartner & Cardon 2004; Hättenschwiler & Gasser 2005), as FD effects depend on the CWM values included in the experiment. This highlights one important perspective in understanding how CWM and FD interact to control ecosystem processes and adds to results found by Makkonen *et al.* (2013) where the direction of the effect of increasing FD in standardized litter water-holding capacity (WHC) on decomposition depended upon the moisture conditions. Higher dissimilarity in WHC increased positive non-additive effects under limiting moisture conditions, whereas under favourable moisture conditions, this led to increased antagonistic non-additive effects (Makkonen *et al.* 2013).

We found that species traits accounted for the majority of the species-specific and community effects on mixed-species decomposition. Nonetheless, some individual species were still found to have a weak, yet statistically significant impact on litter mixture decomposition. This may be due to litter traits not measured in this study, such as polyphenol or tannin content, which can be specifically high in certain species (e.g. *Castanea sativa* or *Quercus* sp.) and could have slightly altered the decomposition expected by the grouping using the five traits considered. However, overall, the assignment of species to decomposability groups was confirmed by the monoculture decomposition data. In addition to this, the overall added amount of variation that individual species explained, after accounting for their traits was small. This indicates that the majority of an individual species' effect on leaf litter mass loss can be explained using the leaf physicochemical traits measured, and monoculture decomposition rate. Increasing the number of traits considered in a study will always provide additional information. However, trait approaches need to be parsimonious (Laughlin 2014), as the number and type of traits measured in a given study are, in most cases, logistically constrained. Here, we show that it is possible to achieve reliable information on litter decomposition in a community using few traits to estimate decomposability groups and elucidate the relative role of CWM and FD of these traits.

In our experiment, there was no significant effect of replacing native species with an exotic species with similar traits on litter mixture decomposition rate, rejecting the assumptions of using the biogeographic origin of a species as a surrogate of its impacts on ecosystem functioning (Buckley & Catford 2016).

On the contrary, we suggest that a trait-based approach, considering a few appropriate and easily measurable leaf traits, can be used to predict the potential impact of both native and exotic species on mixed litter decomposition. We showed that the effect of mixing exotic and native litters depends on how this significantly alters community functional composition. This idea is not limited to the process of decomposition rate of mixed litter, and a similar concept is discussed by Metcalfe, Fisher & Wardle (2011) regarding drivers of soil carbon dioxide efflux. This means that invasive plants can have variable effects within a given environment depending on the traits of the dominant native species present (Poulette & Arthur 2012), also it may help explain why non-additive effects of mixing native and exotic litter has been found not to be consistent (Chen *et al.* 2013). This conclusion indicates that care is needed when predicting potential impacts of exotic species on ecosystems. In contrast to the models predicting the potential impacts of exotic species, which often focus on the traits of exotic species only (Parker *et al.* 1999; Drenovsky *et al.* 2012), it is necessary to account for traits from both the exotic species and the species present at the invaded community. Without considering how similar the traits of native and invasive species are, it will prove more difficult to determine exotic species effects. In particular, it is essential to understand whether exotic species are just adding more of the same traits or whether they are really changing the trait composition of the community by introducing new traits, which, in turn, could result in substantial changes on rates of ecosystem processes. In this way, changes in ecosystem functioning can be expected when exotic species becomes abundant and are functionally different from the native species (Furey *et al.* 2013). Alternatively, some examples also show that even when present in low biomass, exotic species can impact ecosystem processes when possessing values for key traits that are substantially different from native species (Matson 1990; Peltzer *et al.* 2009).

It is worth noting that all exotic species used in this study were within the range of trait values of the native species. It would be valuable to extend this study to consider both the effect of the relative abundance of the species within litter mixtures, as well as to extend the trait dissimilarity within and between exotic and native species in litter mixtures. This would allow us to test how increasingly dissimilar exotic traits impact decomposition, as well as overall litter mixture FD. We do not, however, expect that this will alter the predictions that the effect of introducing, or losing, a species in a community on decomposition depends on how different this species is in traits from the other species in the community. Therefore, the effect of a shift in litter composition will depend on how CWM and FD values in a community will change, irrespective of exotic or native status.

In conclusion, this study gives three important messages that provide an advance in our understanding of the consequences of plant invasions via their functional trait effects on ecosystems. First, while CWM trait value has the greatest effect on litter decomposition, FD in trait values can modulate and interact with CWM effects. FD could therefore not only affect the temporal variation in ecosystem processes (Laliberté

et al. 2010) but also, short-term processes such as mixed-species litter decomposition. Secondly, we demonstrate that litter traits account for most of the species-specific effects on decomposition, with species identity contributing relatively little additional effect beyond that explained by traits alone. Thirdly, exotic species affect processes such as decomposition through their traits and thus might impact ecosystems in the same way as native species, only when altering CWM and FD.

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.k8pp1 (Finerty *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Experimental Design.

Table S1. Native and invasive species preselected according to different decomposition rates (Cornelissen 1996; Wardle, Bonner & Nicholson 1997; Hättenschwiler & Gasser 2005; Halabuk & Gerhátová 2011; Thomas, 1970).

Figure S1. Clusters identify species with similar decomposition rates based on Mg, Ca, C/N content and leaf tension strength. *Indicates species status as exotic.

Table S2. All possible decomposition functional group combinations and the treatment assignments. See main text for details on how treatment levels were assigned.

Figure S2. Calculating Mean (CWM) and Range (FD) values for the 12 possible combinations of decomposability groups (see main text). Four examples (combinations I, K, D and C) are shown here, one combination from within each CWM and FD treatment.

Figure S3. Creating CWM and FD treatments from decomposition groups. Two alternatives were considered a) five treatments: low CWM & low FD (LL), low CWM & high FD (LH), intermediate CWM & high FD (IH), high CWM & low FD (HL) and high CWM & high FD (HH) b) four treatments: low CWM & low FD (LL), low CWM & high FD (LH), high CWM & low FD (HL) and high CWM & high FD (HH).

Figure S4. Mass loss of monoculture litterbags. Colours indicate functional grouping of species; diamonds show mean values of mass loss for each species.

Table S3. Output of linear mixed-effects model describing mass loss of monocultures as a function of decomposition functional groupings. Estimated effect sizes and standard errors are shown for all fixed covariates. Significance reported here refers to post-hoc Tukey test for multiple comparisons. No. observations: 45; grouping factors: Plot, 5, Species, 9.

Appendix S2. Additional Methods.

Data Analyses

Appendix S3. Model Outputs and additional results.

Table S4. Linear mixed-effects model to test for and quantify effects of CWM/FD treatments based on decomposition groups on litter mixture decomposition. Estimated effect sizes and their standard errors are shown for all fixed covariates. *P* values quoted refer to post-hoc Tukey test for multiple comparisons with Bonferroni-adjustments implemented. Estimate value values represent treatment means. L = Low, I = Intermediate, H = H.

Table S5. Comparison of models built on different functional trait effects. All models contain same random effect structure and AIC values quoted are for the maximum likelihood fit (as comparing fixed effects). Functional Diversity is measured as mean pairwise dissimilarity.

Table S6. Linear mixed-effects models describing litter mixture mass loss using physico-chemical leaf traits. Estimated effect sizes and their standard errors are show for all fixed covariates, along with significance of removal of term assessed using likelihood ratio tests (see text).

Table S7. Linear models describing the effect of individual species on model residuals. Estimated effect sizes and their standard errors are show for all fixed covariates, along with significance of removal of term assessed using likelihood ratio tests (see text).

Table S8. Summary of Exotic Effect Analyses.