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# Biogeography of species richness gradients: linking adaptive traits, demography and diversification

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## ABSTRACT

Here we review how adaptive traits contribute to the emergence and maintenance of species richness gradients through their influence on demographic and diversification processes. We start by reviewing how demographic dynamics change along species richness gradients. Empirical studies show that geographical clines in population parameters and measures of demographic variability are frequent along latitudinal and altitudinal gradients. Demographic variability often increases at the extremes of regional species richness gradients and contributes to shape these gradients. Available studies suggest that adaptive traits significantly influence demographic dynamics, and set the limits of species distributions. Traits related to thermal tolerance, resource use, phenology and dispersal seem to play a significant role. For many traits affecting demography and/or diversification processes, complex mechanistic approaches linking genotype, phenotype and fitness are becoming progressively available. In several taxa, species can be distributed along adaptive trait continuums, i.e. a main axis accounting for the bulk of inter-specific variation in some correlated adaptive traits. It is shown that adaptive trait continuums can provide useful mechanistic frameworks to explain demographic dynamics and diversification in species richness gradients. Finally, we review the existence of sequences of adaptive traits in phylogenies, the interactions of adaptive traits and community context, the clinal variation of traits across geographical gradients, and the role of adaptive traits in determining the history of dispersal and diversification of clades. Overall, we show that the study of demographic and evolutionary mechanisms that shape species richness gradients clearly requires the explicit consideration of adaptive traits. To conclude, future research lines and trends in the field are briefly outlined.

*Key words:* adaptive trait, adaptive trait continuum, behaviour, clinal variation, demographic variability, diversification, genomics, phylogeny, species richness gradient, systems biology.

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## I. INTRODUCTION

Species richness gradients are among the most widely discussed patterns in ecology (Hutchinson, 1959; Levinton, 1979; MacArthur & Wilson, 1963; MacArthur, Recher & Cody, 1966; Brown, 1981; Rohde, 1992; Ricklefs, 2004, 2006*a,b*; Hillebrand, 2004). The relative influence of climate-driven demographic responses and long-term clade diversification dynamics in shaping these gradients is still under debate. The ultimate origin and main driver of species richness gradients is found in the long-term processes of speciation and extinction (long-term diversification dynamics) (Mittelbach *et al.*, 2007). In addition, several studies show that present-day demographical processes significantly covary along species richness gradients, determine the presence or absence of species at the local scale, and thus also contribute to reshape and maintain the observed gradients. It is widely acknowledged that adaptive behaviours and trait evolution can profoundly influence both demographic and diversification dynamics (e.g. Pimentel, 1961; Bolker *et al.*, 2003; Huey, Hertz & Sinervo, 2003; Hairston *et al.*, 2005; Coulson *et al.*, 2006; Reed & Levine, 2005; Sol *et al.*, 2005*a*; Sol, Stirling & Lefebvre, 2005*b*; Fletcher, 2006; Abrams, 2006; Fussman, Loreau & Abrams, 2007; Hendry, Nosil & Rieseberg, 2007; Price, 2008; Carnicer, Abrams & Jordano, 2008*a*). However, a detailed and comprehensive review describing the diverse roles played by adaptive traits on the ecological and evolutionary processes that shape species richness gradients is, to our knowledge, currently lacking. Here we intend to fill this gap by reviewing how adaptive traits can shape species richness gradients through their influence on species' demography and diversification dynamics (see Table 1 for a precise definition of adaptive trait). In the first part of this review we examine how demographic dynamics vary along environmental gradients, and how adaptive traits and demographic mechanisms can actively shape species-richness gradients. In the second part we review the evolutionary mechanisms that mould species richness gradients, emphasizing the influence of adaptive behaviours and adaptive traits on diversification rates and the history of dispersal of clades. Finally, we outline and enumerate some possible future research directions for a trait-based evolutionary ecology of species richness gradients. For practical purposes, the review focuses mainly on terrestrial birds and butterflies. These groups have been intensively studied in the field of species richness gradients and are also in the area of expertise of the authors. Where appropriate,

complementary references and examples are provided for plants and other taxonomic groups.

## II. ADAPTIVE TRAITS AND DEMOGRAPHIC DYNAMICS IN SPECIES RICHNESS GRADIENTS

### (1) Demographic dynamics in species richness gradients

The ultimate origin of species richness gradients clearly relies on the long-term processes of speciation, dispersal and extinction of clades (reviewed in Section III). However, present-day demographic processes are continuously modifying local composition, and determine the presence and absence of species at the local scale, and thus persistently maintain, reorganize and reshape species richness gradients. Here we review how demographic processes influence the shape of species-richness gradients.

Species richness gradients have been empirically associated with geographical gradients of diverse environmental variables such as productivity (Jetz & Rahbek, 2002; Hurlbert & Haskell, 2003; H-Acevedo & Currie, 2003; Hawkins *et al.*, 2003*a*; Hawkins, Porter & Diniz-Filho, 2003*b*; Currie *et al.*, 2004; Pautasso & Gaston, 2005; Evans, James & Gaston, 2006; Mönkkönen, Forsman & Bokrna, 2006; Carnicer & Díaz-Delgado, 2008), temperature (Turner, Lennon & Lawrenson, 1988; Currie, 1991; Lennon, Greenwood & Turner, 2000; Jetz & Rahbek, 2002; Forsman & Mönkkönen, 2003; Meehan, Jetz & Brown, 2004; Evans *et al.*, 2006; Carnicer & Díaz-Delgado, 2008), landscape heterogeneity (MacArthur *et al.*, 1966; Lennon *et al.*, 2000; Aauri & de Lucio, 2001; Jetz & Rahbek, 2002; Van Rensburg, Chown & Gaston, 2002; Carnicer & Díaz-Delgado, 2008) or habitat structure (Aauri & de Lucio, 2001; Hurlbert, 2004; Tews *et al.*, 2004; Fuller *et al.*, 2005; Carnicer & Díaz-Delgado, 2008). Recently, Scheiner & Willig (2005) considered the existence of all these diverse associations, and summarized that species richness gradients can be generated by demographic mechanisms if two coupled phenomena occur. First, there is a geographical gradient in one environmental variable (e.g. productivity, habitat availability, temperature, habitat disturbance) or in several spatially correlated environmental variables. Secondly, this environmental gradient causes in turn a geographical gradient in the number of individuals that localities hold (Currie *et al.*, 2004; Scheiner & Willig, 2005; Mönkkönen *et al.*, 2006; Carnicer *et al.*, 2007, 2008*b*; Carnicer & Díaz-Delgado, 2008; Carrascal, Villén-Pérez &

Table 1. Glossary of key concepts and definitions

| Glossary   | References  |
|--|---|
| <b>Trait:</b> a physical, biochemical, morphological, physiological, phenological or behavioural feature measurable at the individual level, from the cell to whole-organism level.  | Violle <i>et al.</i> (2007)   |
| <b>Functional trait:</b> a trait that impacts fitness indirectly <i>via</i> effects on growth, reproduction and survival (or other related demographic performance variables).   | Arnold (1983);<br>Violle <i>et al.</i> (2007);<br>Dalziel <i>et al.</i> (2009)        |
| <b>Adaptive trait:</b> a functional trait with experimentally quantified effects on organism fitness.  | Hodges & Dericg (2009)  |
| <b>Functional/adaptive trait continuum:</b> a significant axis of co-variation between a set of traits observed at the inter-specific level for a taxonomic group, which can be used as a quantitative synthetic measure of life-history variation.  | Wright <i>et al.</i> (2004);<br>Jeschke & Kokko (2009);<br>Chave <i>et al.</i> (2009) |
| <b>Fitness:</b> a quantitative measure that describes the ability to both survive and reproduce, and is equal to the average contribution to the gene pool of the next generation that is made by an average individual of the specified genotype or phenotype.  | Orr (2009)  |
| <b>Trade-off:</b> a linkage between two traits that affects the relative fitness of genotypes and prevents the traits from evolving independently. An increase in fitness due to a change in one trait is opposed by a decrease in fitness due to a concomitant change in a second trait. There are several types of trade-offs like resource allocation trade-offs, resource acquisition trade-offs and specialist-generalist trade-offs. | Angilletta <i>et al.</i> (2003)   |
| <b>Demographic/ecological performance variables:</b> a species-specific measure of the rate of biomass maintained, acquired or moved per unit of time, measured at the individual or population level. Examples of demographic performance variables are survival, mortality, fertility, growth and dispersal. Ecological performance can be also assessed by measuring foraging rates, resource acquisition and predator avoidance rates. | Arnold (1983);<br>Violle <i>et al.</i> (2007);<br>Dalziel <i>et al.</i> (2009)        |
| <b>Demographic dynamics:</b> temporal and spatial variation in the demography (survival, growth, reproduction and dispersal) of individuals and populations.   | Kearney & Porter (2009)   |
| <b>Performance curve:</b> a quantitative description of the variation in demographic performance variables along an environmental gradient.  | Kearney & Porter (2009)   |
| <b>Habitat and niche variables:</b> species-specific quantitative measures of the abiotic conditions (also termed Grinnellian niche) and biotic interactions and resources (also termed Eltonian niche) observed in the localities a species inhabits.   | Soberón (2007)  |
| <b>Trait reaction norm:</b> the set of trait phenotypes produced by a single genotype across a range of environmental conditions or environmental gradient.  | Stearns (1992)  |
| <b>Dispersal sampling effects:</b> changes in the composition and richness of local communities due to the emigration and immigration of individuals.  | Carnicer <i>et al.</i> (2007, 2008b)  |
| <b>Niche filtering/environmental filtering:</b> the process of local extinction of a individual or a subpopulation due to negative trends in its demographic performance (survival, growth and fertility) driven by interactions between species-specific traits and the environment.  | Carnicer <i>et al.</i> (2008b);<br>Levrija-Trejos <i>et al.</i> (2010)                |

Seoanne, 2011; Table 2). In line with these two conditions, a number of empirical studies state that local environmental conditions frequently co-vary with deterministic parameters of populations (e.g. carrying capacities) along environmental or latitudinal gradients (Sæther *et al.*, 2003, 2008). More generally, more productive areas usually sustain higher total population abundances and an increased number of species (Fig. 1; Mönkkönen *et al.*, 2006; Evans *et al.*, 2006). In turn, areas characterized by higher densities usually display greater recruitment *per capita* and per unit of land area (Bock & Jones, 2004). All this empirical evidence suggests the existence of an active causal link between regional demographic dynamics and the shape of species richness gradients.

Moreover, environmental gradients can also influence the variability of local population dynamics (Thomas, Moss & Pollard, 1994; Sæther *et al.*, 2008; Oliver *et al.*, 2010). Localities with reduced community sizes (lower

habitat quality and population abundances) experience increased turnover rates and greater extinction rates and increased effects of demographic stochasticity. All these processes contribute to shape species richness gradients (Fig. 1; Boulinier *et al.*, 1998; Krauss, Steffan-Dewenter & Tschardtke, 2003; Evans, Greenwood & Gaston, 2005a; Evans, Warren & Gaston, 2005b; Carnicer *et al.*, 2007, 2008b; Sæther *et al.*, 2011). Small populations differ markedly in their local dynamics, being affected to a greater extent by Allee effects, inbreeding effects, demographic variability, extinction events and emigration (Kuussaari, Nieminen & Hanski, 1996; Kuussaari *et al.*, 1998; Saccheri *et al.*, 1998; Stephens & Sutherland, 1999; Greene & Stamps, 2001; Orrock & Fletcher, 2005; Melbourne & Hastings, 2008; Sæther *et al.*, 2011).

Environmental gradients and geographic variation in habitat quality (*sensu* Johnson, 2007) may in turn influence

Table 2. A non-exhaustive list of some demographic mechanisms that can potentially shape species richness gradients

| Scale    | Ecological Processes        |   | Theory  |
|----------|-----------------------------|---|---|
| Regional | Regional dispersal dynamics | Sampling effects by dispersal processes                                     | Localities with higher habitat quality usually sustain increased numbers of individuals. Sampling effects produced by species-specific dispersal processes from source areas can shape species richness gradients.  |
|          |                             | Colonization, dispersal and habitat-selection behaviour                     | Colonization and dispersal dynamics are mediated by species-specific habitat selection and dispersal behaviours (adaptive behavioural traits).  |
|          |                             | Niche/habitat filtering   | Local conditions and resources will interact with the adaptive traits of species, influence their local demographic and dispersal rates and filter the species that are incorporated from regional pools or source regions.   |
| Local    | Demographic dynamics        | Demographic effects of environmental conditions                             | Effects of environmental variables on deterministic components of population dynamics (e.g. carrying capacity, survival) originate geographical gradients in abundance and shape species richness gradients.  |
|          |                             | Abundance-extinction dynamics (demographic and environmental stochasticity) | Increased negative effects of demographic variability in localities with reduced community size and small population sizes increase extinction risk and shape species richness gradients (e.g. Fig. 2). Extinction risk is usually higher in species with specialized adaptive traits and lifestyles (e.g. Koh <i>et al.</i> , 2004; Kotiaho <i>et al.</i> , 2005). Long-term demographic dynamics that sustain species-richness gradients are influenced by species-specific adaptive traits (e.g. Fig. 3B). |
|          |                             | Local interactions  | Interactions between species, resources and environmental conditions limit/enhance local population persistence, define local composition and limit species' ranges.  |

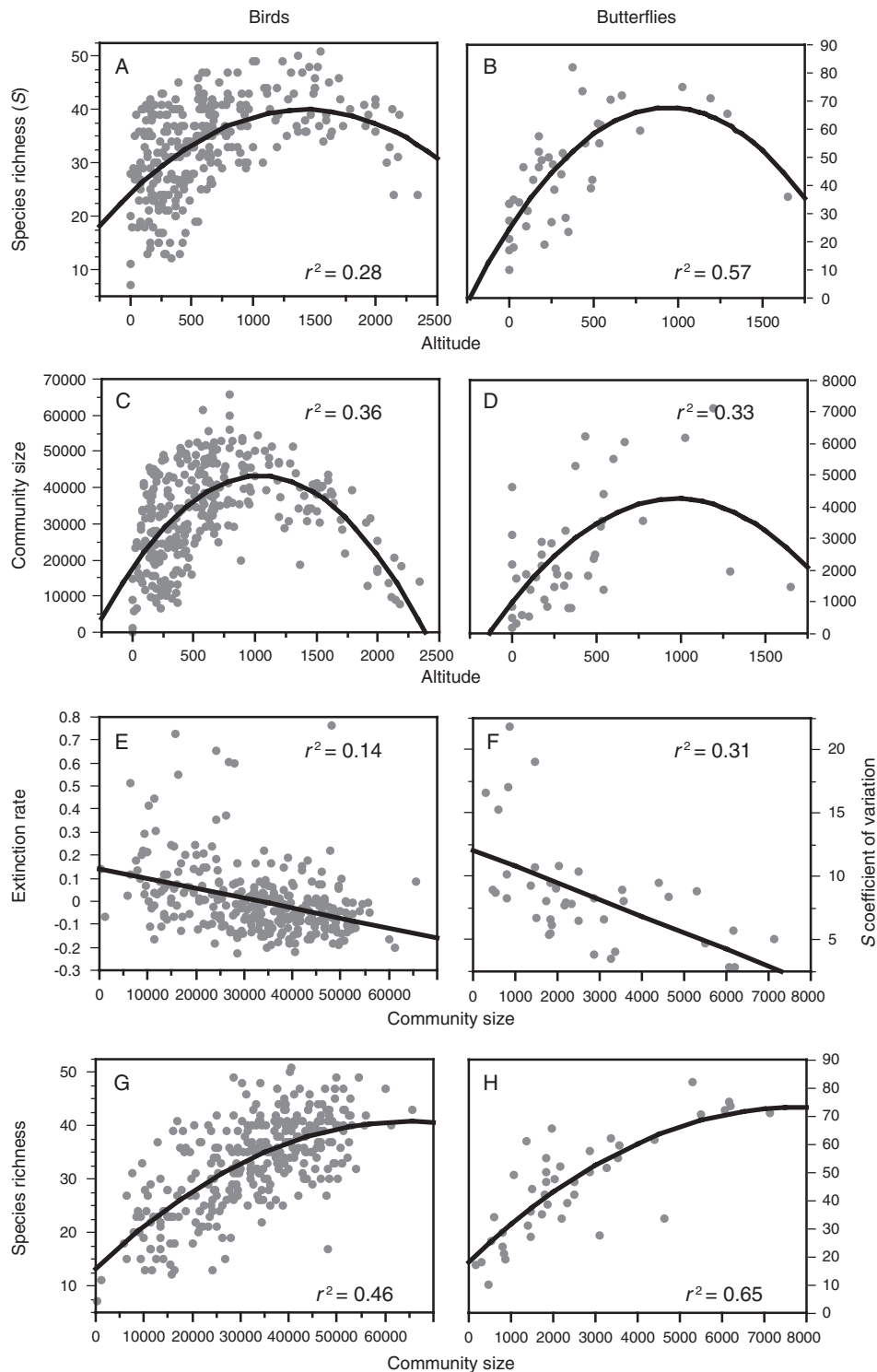
regional dispersal dynamics (Paradis *et al.*, 1998; Parejo *et al.*, 2007; Studds, Kyser & Marra, 2008; Baguette, Clobert & Schtickzelle, 2011; Alexander *et al.*, 2011). Localities with smaller community sizes (i.e. lower habitat quality and reduced total number of individuals) are expected to hold a reduced number of species by dispersal-limited sampling from more productive source areas in theoretical models (Hubbell, 2001; Vellend, 2005). These trends are supported by empirical studies (Coleman *et al.*, 1982; Carnicer *et al.*, 2007, 2008*b*; Honkanen *et al.*, 2011; Alexander *et al.*, 2011; Kraft *et al.*, 2011). Remarkably, these dispersal-limited sampling effects are also significantly influenced by the number of species available in the different biogeographic pools that contribute to a specific locality (e.g. Pärtel, 2002; Pärtel, Laanisto & Zobel, 2007; Kozak & Wiens, 2010; Grace, Harrison & Damschen, 2011). Widespread and abundant generalists are more prone to successfully colonizing localities with low community sizes whereas less-abundant species (at the regional level) are more frequently absent (Fig. 2; Carnicer *et al.*, 2008*b*; Alexander *et al.*, 2011). The coexistence of habitat-generalist and -specialist strategies can produce spatially nested patterns in the distributions of the species that finally shape regional gradients (Fig. 2). Several studies indicate that the temporal demographic dynamics of widespread habitat generalists and rare habitat specialists are qualitatively different. Demographic dynamics of populations of widespread and abundant habitat generalists tend to co-vary synchronously at larger scales, tracking large-scale environmental variation, whereas

different small populations of rare species and habitat specialists often vary asynchronously, are much more affected by demographic stochasticity and are less synchronized with environmental variation (Hanski & Woiwod, 1993; Sutcliffe, Thomas & Moss, 1996; Sæther *et al.*, 2011).

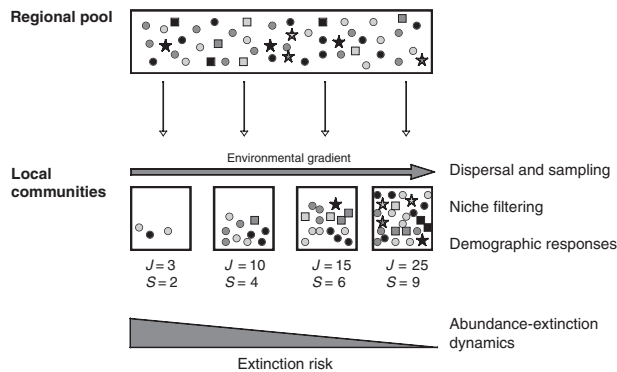
## (2) Adaptive traits and demographic dynamics

Population dynamics can be strongly influenced by adaptive behaviours and traits (Koh, Sodhi & Brook, 2004; Kotiaho *et al.*, 2005; Helm, Piersma & van der Jeugd, 2006; Hanski & Saccheri, 2006; Poorter *et al.*, 2008; Hoffmann, 2010; Hanski & Mononen, 2011). Colonization rates, extinction events and demographic rates are influenced by species adaptations in habitat selection behaviour, dispersal behaviour, niche breadth and life-history traits (Brändle *et al.*, 2002; Wiens & Donoghue, 2004; Sol *et al.*, 2005*a*; Sol, Stirling & Lefebvre, 2005*b*; Carnicer *et al.*, 2008*b*; Sæther *et al.*, 2011, Hanski & Mononen, 2011). Arguably, a limited set of species-specific adaptive traits should regulate the demographic dynamics that limit species distributions and eventually shape species richness gradients. Available studies suggest that in many cases a significant role is played by traits related to thermal or aridity tolerance, host-plant or resource use, phenology and dispersal (e.g. Kellermann *et al.*, 2009; Chuine, 2010; Stefanescu, Carnicer & Peñuelas, 2011*a*). For instance, experimental studies indicate that low genetic variation on thermal adaptive traits can reduce population growth and determine higher extinction risk in localities near the





**Fig. 1.** Parallel altitudinal species-richness gradients of butterflies and forest birds in Catalonia (Spain). (A, B) Altitudinal variation of bird and butterfly species richness. (C, D) Altitudinal variation of community size (total number of individuals of birds and butterflies, respectively). (E, F) Observed abundance-extinction dynamics for birds and butterflies: (E) reduction in the proportion of forest bird species that became locally extinct with increased community size; (F) observed decrease in the temporal coefficient of variation of butterfly species richness with increased community size. Bird extinction numbers were calculated comparing two separate field survey periods: 1980–83 and 1999–2002 (Carnicer *et al.*, 2007). The temporal coefficient of variation of butterfly species richness was calculated from annual surveys for the 1988–2007 time period. (G, H) Observed relationships between species richness and community size for birds and butterflies. All fitted models were significant with  $P < 0.0001$ .



**Fig. 2.** An illustrative scheme explaining how regional dispersal dynamics (i.e. local sampling by dispersal processes), niche-filtering and local population dynamics can shape species-richness gradients at the regional scale. Stars, circles and squares represent individuals of different species. Each species is represented by a unique combination of shape and shading. The environmental gradient originates a gradient in the total number of individuals that localities hold (community size or  $J$ ). Localities with greater community sizes ( $J$ ) may sustain increased species richness ( $S$ ) by local positive demographic responses and by dispersal sampling effects from other source areas. Widespread and abundant species (circles) are preferentially included in localities with low community sizes (low-quality sites). Squares represent species with intermediate life histories between specialist and generalist lifestyles. Niche filtering occurs in species with more selective habitat preferences (stars). Note that habitat specialists (stars) colonize only specific environments (high- $J$  localities) whereas generalists (circles) occupy different types of localities (high- and low- $J$  localities) leading to a geographically nested structure. Localities with extreme environmental conditions sustain small population sizes. This increases the extinction risk of populations and may cause an additional decrease in local species richness (abundance-extinction dynamics).

thermal tolerance limit of the species (Willi & Hoffmann, 2009; Hoffmann, 2010). Similarly, low heritable variation and low evolvability in thermal adaptive traits is associated with the limits of the geographical distributions of insects (Kellermann *et al.*, 2009; Hoffmann, 2010).

Phenological traits also influence reproductive rates and survival at the limits of species distributions (Chaine, 2010; Visser *et al.*, 2010). Phenological traits are usually integrated in complex schedules, i.e. seasonally ordered annual sequences of behaviours that are genetically programmed (Helm *et al.*, 2006; Salewski & Bruderer 2007; Wikelski *et al.*, 2008; Liedvogel *et al.*, 2009; Visser *et al.*, 2010) and plastically adjusted by some environmental and social cues perceived by species (e.g. Doligez *et al.*, 2003; Helm *et al.*, 2006; Fletcher, 2007; Forsman *et al.*, 2008; Studds *et al.*, 2008; Visser *et al.*, 2010). For instance, in birds, behavioural schedules can include autumn and spring migration, breeding and territorial behaviour, natal and adult dispersal, moult, and wintering flocking. Interestingly, available studies suggest important effects of bird behavioural schedules in the seasonal and spatial variance of patterns

of species richness gradients (e.g. effects of migration in bird species richness gradients; Hurlbert & Haskell, 2003; Carnicer & Díaz-Delgado, 2008). Similarly, important effects of insect diapause and phenology are detected on latitudinal and altitudinal distributions (e.g. Schmidt & Paaby, 2008).

Diverse adaptive traits and behaviours can strongly determine dispersal capacities and thus may determine sampling effects and the shape of regional species richness gradients (Table 2). Some examples of these adaptive behaviours are conspecific and heterospecific attraction and repulsion, public information gathering, and species-specific behavioural barriers to dispersal. Moreover, many species have evolutionarily developed condition-dependent dispersal strategies (Bowler & Benton, 2005; Clobert *et al.*, 2009), and plastically respond to the spatial and temporal variation of the costs of dispersal. For example, empirical studies in a number of bird species assert that breeding dispersal and settlement can be behaviourally driven by public information gathered by postfledging juveniles and adults to assess the suitability of future breeding sites (Doligez, Danchin & Clobert, 2002; Doligez *et al.*, 2003; Danchin *et al.*, 2004; Dall *et al.*, 2005; Parejo *et al.*, 2007). In making settlement decisions, birds evaluate diverse cues like local food availability (Tellería, Ramírez & Pérez-Tris, 2008; Forsman *et al.*, 2008), competitor density (Forsman *et al.*, 2008) and local predation risk (Harris & Reed, 2002; Thomson *et al.*, 2006). Condition-dependent dispersal responses are also observed in butterflies, insects and other taxonomic groups (Clobert *et al.*, 2009; Baguette *et al.*, 2011).

On the other hand dispersal is restricted by species-specific behavioural barriers (Reed, 1999; Ries & Debinski, 2001; Harris & Reed, 2002; Koh *et al.*, 2004; Kotiaho *et al.*, 2005; Reed & Levine, 2005; Clobert *et al.*, 2009). Habitat fragmentation, gaps and ecotones can be more common at the extremes of regional species richness gradients (e.g. Carnicer *et al.*, 2007) and are frequently perceived as barriers to movement by some species but not for others (Desrochers & Hannon, 1997; Ries & Debinski, 2001) because species are characterized by specific threshold distances to movement across certain habitat types (Harris & Reed, 2002; Moore *et al.*, 2008). Generally, behavioural barriers to dispersal vary among functional groups, being usually greater in habitat specialists and resident species (Haddad & Baum, 1999; Desrochers & Hannon, 1997; Ries & Debinski, 2001; Harris & Reed, 2002; Kotiaho *et al.*, 2005). Finally, phenotypic plasticity and heritable variation on dispersal capacity is frequent at both the intra- and inter-specific level. Indeed, both aspects have been extensively documented, influencing population dynamics and range-expansion processes (Thomas *et al.*, 2001; Ovaskainen *et al.*, 2008; Niitpöld *et al.*, 2009; Clobert *et al.*, 2009; Stevens, Turlure & Baguette, 2010).

Overall, a number of adaptive behaviours and traits can cause spatial aggregative responses, promote dispersal processes and determine dispersal dynamics along regional species richness gradients; but are rarely considered in the macroecological analyses of regional species richness

gradients. Moreover, theoretical studies indicate that population dynamics that shape species richness gradients at local or regional scales may be substantially influenced by these behavioural adaptive traits. For instance, behaviours such as conspecific and heterospecific attraction displayed during breeding and habitat selection (Stamps, 1988, 1991; Mönkkönen, Helle & Soppela, 1990; Fletcher, 2007) can profoundly influence metapopulation source-sink dynamics (e.g. Reed, 1999; Sæther, Engen & Lande, 1999; Greene & Stamps, 2001; Greene, 2003; Reed & Levine, 2005; Fletcher, 2006, 2007). Generally, theoretical models that incorporate conspecific aggregative responses produce an increase in extinction rates and reductions in colonization rates, leading to metapopulations with reduced viability. Individuals that display conspecific attraction behaviour tend to immigrate into already occupied patches, decreasing the colonization rate of empty patches. On the other hand, models with conspecific repulsion confer higher viability to modeled metapopulations (Bowler & Benton, 2005). Similarly, Reed & Levine (2005) modelled metapopulation persistence based on diverse species-specific behaviours that influence colonization, extinction and rescue effects. In sum, available empirical and theoretical evidence suggests that dispersal along species-richness gradients is usually a non-random process in which species-specific adaptive traits, behavioural responses and condition-dependent responses play a major role.

Local population dynamics, regional dispersal dynamics, evolutionary dynamics of adaptive traits and diversification processes are not independent processes (Johnson & Stinchcombe, 2007; Fussman *et al.*, 2007). For instance, behavioural and morphological traits affecting dispersal capacity (Böhning-Gaese, González-Guzmán & Brown, 1998; Böhning-Gaese *et al.*, 2006) and niche breadth (Brändle *et al.*, 2002) might shape species richness gradients through both demographic and evolutionary dynamics. Indeed, the effect of such adaptive traits is twofold: demographically, they determine differences in species colonizing, extinction and population growth rates that actively shape present-day gradients (Table 2; Wiens & Donoghue, 2004; Wiens & Graham, 2005; Hanski & Saccheri, 2006; Kotiaho *et al.*, 2005); evolutionarily, they may determine gene flow and long-term diversification dynamics (Phillimore *et al.*, 2006; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010). For instance, existing empirical evidence states that clades with increased dispersal abilities are more able to both expand their ranges and diversify (Böhning-Gaese *et al.*, 2006; Phillimore *et al.*, 2006, 2007; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010; but see Belliure *et al.*, 2000).

### III. ADAPTIVE TRAITS AND DIVERSIFICATION DYNAMICS IN SPECIES RICHNESS GRADIENTS

Species richness gradients can be generated by evolutionary mechanisms *via* geographical gradients in different variables: speciation rates (Cardillo, 1999; Fjeldsa & Rahbek, 2006; Weir, 2006; Ricklefs, 2006b; Weir & Schluter, 2007),

lineage extinction rates (Hawkins *et al.*, 2007; Wiens, 2007), geographical area suitable for speciation (Rosenzweig, 1995; Pärtel *et al.*, 2007; Fine & Ree, 2006; Vamosi & Vamosi, 2010; Zobel *et al.*, 2011), time to diversify (Stephens & Wiens, 2003; Fine & Ree, 2006; Benton & Emerson, 2007; Hawkins *et al.*, 2007; Wiens, Pyron & Moen, 2011) and historical dispersal clines (Hawkins *et al.*, 2007; Roy & Goldberg, 2007; Wiens, 2007). All these processes may be influenced by the adaptive traits of species and their lifestyles (Table 3). For instance, adaptive traits can influence speciation and extinction rates (Kotiaho *et al.*, 2005; Rabosky, 2009; Vamosi & Vamosi, 2010) and influence historical dispersal clines (Van Bocxlaer *et al.*, 2010).

A latitudinal gradient of increasing diversification rates with decreasing latitude has been described empirically in birds, butterflies, plants and other groups (Cardillo, 1999; Ricklefs, 2006b; Wright, Keeling & Gillman, 2006; Weir & Schluter, 2007; Wiens, 2007). However, the relative importance of lineage extinction rates, speciation rates, area, time and dispersal movements in generating species richness gradients is not well understood yet (Weir, 2006; Hawkins *et al.*, 2007; Wiens, 2007; Weir & Schluter, 2007). Available evidence suggests that all these processes are effectively contributing to the generation of the latitudinal gradients of species richness (Goldberg *et al.*, 2005; Fjeldsa & Rahbek, 2006; Hawkins *et al.*, 2007; Wiens, 2007; Roy & Goldberg, 2007; Van Bocxlaer *et al.*, 2010) and therefore the debate is centred in contrasting and evaluating the relative importance of all the processes listed in Table 3. Below we elaborate on those research areas that are needed to achieve a more precise view of the role of adaptive traits on the evolutionary processes that affect species richness gradients.

#### (1) Genetic basis of adaptive traits—mechanistic approaches linking genotype, phenotype and fitness

The application of genomics and high-throughput techniques greatly facilitates the identification of the genes underlying ecologically important traits (e.g. Vasemägi & Primmer, 2005; Hoekstra *et al.*, 2006; Jensen, Wong & Aquadro, 2007; Naish & Hard, 2008; Ellegren & Sheldon, 2008; Pavlidis, Hutter & Stephan, 2008; Stinchcombe & Hoekstra, 2008; Slate *et al.*, 2009), and the identification of genes and traits specifically involved in speciation and reproductive isolation (Schluter, 2009; Wolf, Lindsell & Backström, 2010; Presgraves, 2010; Backström *et al.*, 2010; Rieseberg & Blackman, 2010; Nosil & Schluter, 2011; Rice *et al.*, 2011). Moreover, in a quite reduced number of well-described adaptive traits, mechanistic approaches linking genotype, phenotype and fitness effects can be implemented (reviewed in Dalziel, Rogers & Schulte, 2009). These approaches provide descriptions of adaptive traits at several hierarchical levels (genetic variation, protein function, biochemical networks, neuro-molecular and hormonal function, whole-organism behavioural and physiological performance, and fitness differences) (Dalziel *et al.*, 2009; Dillon *et al.*, 2009; Palsson, 2009). Notably, these complex approaches are becoming progressively available for some adaptive traits that



Table 3. A non-exhaustive list of some evolutionary mechanisms that can potentially influence species richness gradients

| Scale    | Evolutionary processes                                    | Theory   |
|----------|---|--|
| Regional | Geographic mosaics of selection and speciation rates      | Geographic differences in selection can promote differences in speciation rates between areas and potentially originate clines in species richness. Rates of speciation can be increased or reduced by clade-specific adaptive traits (Sargent, 2004) and by the interaction of adaptive traits and the environment (De Queiroz, 2002).  |
|          | Geographic mosaics in extinction rates                    | Extinction risk can vary geographically. Increased lineage extinction rates due to regional climate and vegetation shifts can create gradients in species richness. Rates of extinction are significantly influenced by the adaptive traits of species, being usually higher in specialized lifestyles (e.g. Kotiaho <i>et al.</i> , 2005).  |
|          | Diversification area                                      | Larger habitat areas may allow for increased total diversification rates and higher species richness.  |
|          | Diversification time                                      | Larger diversification time in the tropics and other areas may have produced increased cumulative diversification rates.   |
|          | Historical dispersal clines                               | Historical dispersal clines from centres of diversification yield to species richness clines with maximum values usually near the origin point. Adaptive traits associated with dispersal and trophic generalism explain differences in historical dispersal clines of clades (Moyle <i>et al.</i> , 2009; Van Bocxlaer <i>et al.</i> , 2010).   |
|          | Range expansion, isolation and allopatric diversification | Topographic barriers can facilitate the emergence of species-richness gradients if populations of formerly widespread species become isolated by mountain chains or other geographical barriers and diversify by independent evolutionary paths and local adaptation.  |
|          | Specialist/generalist transition dynamics                 | Diversification dynamics often oscillate between range expansion phases (often associated with the geographical expansion of clades characterized by high-dispersal and generalist adaptive traits) and specialization phases (often associated with the emergence of more specialized adaptive traits and local specialization) (Janz & Nylin, 2008; Moyle <i>et al.</i> , 2009; Van Bocxlaer <i>et al.</i> , 2010). A latitudinal increase of the proportion of specialists has been detected in some groups (Scriber, 1973; Dyer <i>et al.</i> , 2007). Specialist-generalist life history variation can be synthetically described by adaptive trait continuums in some clades (e.g. Fig 3). |
| Local    | Community context   | Geographical gradients of local interactions, such as competition, parasitism, facilitation, predation or mutualism, can promote divergent or convergent selection on adaptive traits, influence extinction and diversification rates and shape species-richness gradients.  |
|          | Uneven spatio-temporal distribution of resources          | Uneven spatiotemporal distribution of resources promotes the emergence of different adaptive foraging behavioural strategies and phenologies, the emergence of migratory behaviours, drives diversification processes and contributes to shape species-richness gradients.   |
|          | Phenotypically plastic responses                          | Phenotypically plastic responses drive local selection pressures on adaptive traits and influence diversification processes.   |

determine species' ranges and the shape of species-richness gradients, like thermal preference and aridity tolerance (Dillon *et al.*, 2009; Kellermann *et al.*, 2009; Hoffmann, 2010; Paaby *et al.*, 2010), phenological traits (Flowers *et al.*, 2009; Chuine, 2010; Visser *et al.*, 2010) and dispersal capacity (Dalziel *et al.*, 2009; Wheat *et al.*, 2011). Similarly, integrative descriptions of suites of traits involved in the emergence of reproductive isolation and speciation are becoming available for plants, birds, butterflies, and other groups (Bradshaw & Schemske, 2003; Shapiro *et al.*, 2004; Kronforst *et al.*, 2006; Abzhanov *et al.*, 2006; Seehausen *et al.*, 2008; Hodges & Derieg, 2009; Chamberlain *et al.*, 2009; Bomblies & Weigel, 2010; Wolf *et al.*, 2010; Baxter *et al.*, 2010; Hohenlohe *et al.*, 2010; McBride & Singer, 2010; Sætre & Sæther, 2010). Interestingly, these integrative mechanistic approaches can be successfully applied to the study of the evolutionary processes in species richness gradients (Table 3), for example specifically allowing the study of speciation processes along environmental gradients. For instance, Seehausen *et al.* (2008) studied the species of cichlid fishes distributed along

several replicated environmental gradients in the islands of Lake Victoria. After several years of combined field, experimental and molecular studies, they were able to quantify precisely a suite of traits at several hierarchical levels of organization (ecological, behavioural and molecular traits) that experienced divergent evolution and were significantly associated with reproductive isolation and sympatric speciation in these gradients. Notably, differences in the slope of the environmental gradients in Lake Victoria explained the observed variation in the progress and completeness of speciation: speciation occurred on all but the steepest gradients (Seehausen *et al.*, 2008). Remarkably, these empirical trends fully matched recent theoretical models of clinal speciation predicting the emergence of speciation at environmental gradients of intermediate slopes (Doebeli & Dieckmann, 2003; Heinz, Mazzucco & Dieckmann, 2009).

## (2) Sequences of adaptive traits along phylogenies

Molecular phylogenetic studies frequently report specific traits (often called key innovations) significantly associated

with the emergence of adaptive radiations and speciation events (Heard & Hauser, 1995; Webb *et al.*, 2002; Ree, 2005; Vitt & Pianka, 2005; Paradis, 2005; Donoghue, 2005; Ackerly, Schwilk & Webb, 2006; Wheat *et al.*, 2007; Seehausen *et al.*, 2008; Menken, Boomsma & Van Nieuwerkerken, 2009; Hodges & Dierig, 2009; Wolf *et al.*, 2010; Glor, 2010). For instance, Streebman & Danley (2003) highlighted that vertebrate radiations usually follow similar trajectories, diverging first in characters associated with habitat selection, then in foraging morphology and finally in communication or sexually related traits. The general model pointed out by Streebman & Danley (2003) has empirical support in some bird clades, as morphological shifts in bird characters associated with habitat use can usually be traced to the most internal nodes of the phylogeny in a number of clades (Desrochers & Diamond, 1986; Richman, 1996; Price, 1998; Ricklefs, 2007). Subsequent diversifications in some bird phylogenies are then based on traits associated with foraging behaviour and resource-tracking movements, such as beak shape, body size and wing length (Price, 1998; Remsen, 2003; Burns, Hackett & Klein, 2003; Ricklefs, 2007). However, this general scheme of diversification is likely to apply only in some cases and should be observed with caution for several reasons. First, some studies document the possibility of rapid evolution in morphological traits associated with habitat and resource use, suggesting again that trait sequences might easily differ among clades (Böhning-Gaese & Oberrath, 1999; Smith *et al.*, 1997; Böhning-Gaese, Schuda & Helbig, 2003). Second, trait sequences implied in diversification possibly are much more complex than the evolutionary hypothetical sequences outlined until now (e.g. Price, 1998) and might be site specific. For instance, apart from foraging and habitat-use traits, a considerable number of additional traits have been found to be involved in bird speciation processes (Table 4). Third, a variety of different processes not associated with species traits can influence speciation rates in a non-sequential manner.

In Lepidoptera, Menken *et al.* (2009) recently described a phylogenetic sequence of key adaptive traits. Initial diversifications are related to a trophic switch from litter feeding to leaf herbivory, and with the emergence of internal larval feeding (e.g. mining, galling, boring) and monophagous diets. Later, derived adaptive traits related to the evolution of exposed feeding (e.g. larval locomotory morphology, desiccation tolerance, larval size, digestive metabolism) and larval generalist feeding progressively increase in frequency along the phylogeny, albeit with frequent reversals and specialist-generalist transitions (*sensu* Janz & Nylin, 2008).

In the case of plants, Donoghue (2005) has reviewed which sequences of key adaptive traits occurred at the initial splits of plant phylogenies; and Ackerly *et al.* (2006) highlighted that small-scale components of the niche that differ among co-occurring species (such as microhabitat use) usually diverge early in the phylogeny during adaptive radiations in plants. At more derived levels of plant phylogenies, higher speciation rates are often positively associated with biotic pollination

and floral asymmetry (Sargent, 2004; Vamosi & Vamosi, 2010), herbaceous life form (Ricklefs & Renner, 1994; Vamosi & Vamosi, 2010), shorter generation times (Smith & Donoghue, 2008) and self-incompatibility (Igic, Lande & Kohn, 2008; Goldberg *et al.*, 2010), and negatively associated with dioecy (Heilbut, 2000).

Overall, a considerable number of traits have been associated with diversification processes in different taxonomic groups and in some clades can be ordered sequentially providing some initial evolutionary hypotheses. Of course, much more detailed phylogenetic analyses are yet required to derive a general quantitative perspective of the sequential order and importance of traits implied in each specific group and geographic site (Ree, 2005; Paradis, 2005; Phillimore *et al.*, 2007; Menken *et al.*, 2009; Kozak & Wiens, 2011), and the genetic and developmental paths involved in the regulation of these traits (Wu *et al.*, 2004; Abzhanov *et al.*, 2004; Fitzpatrick *et al.*, 2005; Donoghue, 2005). Nevertheless, some pioneering studies show the potential of multi-trait comparative phylogenetic studies in explaining worldwide radiations and diversity patterns for a determinate taxonomic group. For instance, van Boxclaeer *et al.* (2010) used a multiple-trait comparative phylogenetic analysis to study the evolution of highly dispersive and low-dispersive toad species during the last 55 million years. This study covered 228 taxa (43% of extant bufonid species diversity) distributed worldwide. Their analysis allowed the identification of an optimal range-expansion phenotype, based on a suite of traits (body size, presence of inguinal fat bodies, aquatic and opportunistic oviposition site, large clutch size and exotrophic larvae) and habitat-use variables (semi-terrestrial adult habitat). Interestingly, van Boxclaeer *et al.* (2010) were able to: (1) provide a worldwide reconstruction of the more plausible history of phenotype evolution for the bufonid clade, (2) link changes in multi-trait phenotype evolution with the temporal dynamics of diversification rates during the last 55 million years, (3) significantly associate the observed increases in estimates of net diversification rates during the Eocene and Oligocene with the emergence of a highly dispersive multi-trait phenotype, and (4) explain the worldwide geographic expansion of the bufonid clade. Overall, this pioneering study provided a worldwide synthetic view of how trait evolution moulded the geographic diversification of toads during the last 55 million years in time and space.

### (3) The role of adaptive traits in the history of biogeographical movements of clades

The consideration of historical diversification centres and clade historical dispersal clines is essential for the understanding of the historical generation of global and regional species richness gradients (e.g. Ericson, Irestedt & Johansson, 2003; Hawkins *et al.*, 2007; Roy & Goldberg, 2007). Episodes of biogeographic movement and/or isolation are in some cases associated with clear shifts in the diversification rates of clades (Moore & Donoghue, 2007). For example, empirical evidence supports that colonization of mountain chains

Table 4. Some adaptive traits associated with speciation in birds

|                                 |  |
|---------------------------------|--|
| <b>Habitat selection traits</b> | Morphological traits associated with habitat-use behaviour differ among some bird clades during the initial splits of the phylogeny (Desrochers & Diamond, 1986; Price, 1998; Ricklefs, 2007).   |
| <b>Size and foraging traits</b> | After this initial divergence in habitat-use-related traits, subsequent diversifications are usually based on body size and/or traits associated with foraging behaviour (Price, 1998).  |
| <b>Dispersal traits</b>         | Traits that enhance dispersal, colonization and migration can have long-term effects on the diversification dynamics of clades (Böhning-Gaese <i>et al.</i> , 1998; Irwin & Irwin, 2005; Phillimore <i>et al.</i> , 2007; Moyle <i>et al.</i> , 2009). For instance, the number of bird subspecies covaries with migratory habits and geographical range size (Bellire <i>et al.</i> , 2000; Phillimore <i>et al.</i> , 2007). Traits associated with enhanced dispersal and migratory ability possibly evolved from local-area feeding strategies such as seasonal resource tracking and altitudinal movements (Levey & Stiles, 1992; Mettke-Hofmann & Gwinner, 2004; Boyle & Conway, 2007; Carnicer <i>et al.</i> , 2008a). Subsequently, such behaviours could potentially have facilitated colonization, range expansion and allopatric diversification processes in a number of bird clades (Irwin & Irwin, 2005; Phillimore <i>et al.</i> , 2006; Böhning-Gaese <i>et al.</i> , 2006; Moyle <i>et al.</i> , 2009).   |
| <b>Mate-choice traits</b>       | Geographical divergence in characters involved in mate choice, such as song, plumage, and behavioural displays are likely to play important roles in avian speciation (Møller & Cuervo, 1998; Edwards <i>et al.</i> , 2005), albeit some authors have suggested that the role is secondary when compared with other factors such as dispersal, range size or feeding generalization (Price, 1998; Phillimore <i>et al.</i> , 2006). Gradual divergence of song in allopatric populations may result in reproductive isolation upon secondary contact and speciation (Grant & Grant, 1997; Irwin, 2000; Irwin <i>et al.</i> , 2001a,b, 2005; Edwards <i>et al.</i> , 2005; Toews & Irwin, 2008). Songs have been found to diverge as a result of habitat-dependent selection or indirectly as a consequence of morphological adaptations (Podos, 2001; Slabbekoorn & Smith, 2002a,b; Patten <i>et al.</i> , 2004; Seddon, 2005). Other studies, however, support the importance of stochastic evolution of songs in the evolution of new species (Miyasato & Baker, 1999; Irwin <i>et al.</i> , 2008). In some specific clades, song can act as a key character determining diversification dynamics. Indeed, song learning and sexual imprinting explain the sympatric diversification of brood parasitic indigobirds (Sorenson <i>et al.</i> , 2003). Similarly, sexually selected traits predict patterns of species richness in antbirds (Seddon <i>et al.</i> , 2008). |
| <b>Cognitive traits</b>         | A larger relative brain size has been found to enhance bird cognitive skills thus promoting feeding generalization and enabling the use of new resources (Lefebvre <i>et al.</i> , 1997). This increase in phenotypic plasticity in big-brained birds can increase diversification rates by two causal paths. First, increased relative brain size has been found to allow birds to shift to new adaptive zones thus promoting morphological diversification (Wyles <i>et al.</i> , 1983; Sol <i>et al.</i> , 2005b; Sol & Price, 2008). Second, big-brained individuals might more easily spread to new locations increasing opportunities for allopatric speciation and reducing extinction risk (Sol <i>et al.</i> , 2002, 2005a,b; Sol & Price, 2008).   |

favoured isolation and strongly increased diversification rates in birds, butterflies, plants and other taxa (Weir, 2006; Fjeldsa & Rahbek, 2006; Hughes & Eastwood, 2006; Johansson *et al.*, 2007; Moore & Donoghue, 2007; Price, 2008). Jablonski, Roy & Valentine (2006) proposed a general verbal model of global diversification (the “Out of the Tropics” model) in which the bulk of the clades preferentially originate in the tropics and only some of them expand towards the poles leading to secondary diversification processes there. This general scheme matches the observed phylogenetic trends in bird and butterfly species richness-gradients at a global scale (Hawkins *et al.*, 2007; Hawkins, 2010), although exceptions exist and are to be expected in a number of clades (Ericson *et al.*, 2003; Wiens, 2007). Similarly, in the Passerida clade a longitudinal gradient in species richness from their centres of diversification in South East Asia has been described, presumably reflecting both an historical dispersal cline and a time-for-speciation effect (Hawkins *et al.*, 2007). Elsewhere, Richman (1996) showed that *Phylloscopus* warblers spread by multiple invasions from mainland Asia, with only limited subsequent speciation and little associated morphological diversification. Notably, some pioneering studies are starting

to analyze the role of adaptive traits in these historical processes of range expansion and diversification (Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010). These studies suggest that the acquisition of traits associated with a high dispersal capacity and a generalist trophic position play a major role on range expansion phases. Range expansion phases are in some cases followed by subsequent phases of local specialization and speciation, in which adaptive traits associated with specialist life histories evolve (e.g. Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010). Similarly, in some ectotherm clades like salamanders, the acquisition of higher metabolic rates is associated with increased dispersal capacity, broader thermal tolerance and the expansion of distributional ranges (Bernardo *et al.*, 2007). Genetic links between dispersal capacity, metabolic rate, population growth rate, and range distribution of insects have also been documented (reviewed in Dalziel *et al.*, 2009). Together, this body of empirical evidence indicates that adaptive traits mediate specialist-generalist transitions, promote range expansion phases and influence the dynamics of diversification during the dispersal of clades (Janz & Nylin, 2008; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010; Vamosi & Vamosi, 2010).

#### (4) Clinal variation of adaptive traits

The study of clinal variation of adaptive traits along parallel environmental gradients provides an ideal scenario to examine how trait-environment interactions may limit species' distributions, and thus contribute to shape species-richness gradients (Schmidt *et al.*, 2008a; Kolaczowski *et al.*, 2011). Latitudinal, altitudinal and regional clines along environmental gradients have been observed for adaptive traits and genetic markers related to thermal tolerance (Watt, 1983; Rank & Dahloff, 2002; Hoffmann, Shirriffs & Scott, 2005; Kyriacou *et al.*, 2008; Collinge *et al.*, 2008; Fry, Donlon & Saweikis, 2008; Karl, Schmitt & Fisher, 2009; Paaby *et al.*, 2010), phenological traits (Masaki, 1999; Stinchcombe *et al.*, 2004; Schmidt *et al.*, 2008b), dispersal capacity (Haag *et al.*, 2005; Saastamoinen & Hanski, 2008) and life-history traits (Schmidt & Paaby, 2008; Klemme & Hanski, 2009; Paaby *et al.*, 2010; Montesinos-Navarro *et al.*, 2011). The study of geographic clines in multiple genetic markers allows the identification of candidate genes implied in the regulation of adaptive traits that interact with environmental gradients and probably contribute to determine the distribution of species along them (Schmidt *et al.*, 2008a; Blackman, 2010; Paaby *et al.*, 2010). Interestingly, these studies of adaptive clinal variation can be performed at multiple spatial scales, ranging from local-scale gradients to latitudinal clines (e.g. Schmidt *et al.*, 2008a). Moreover, they allow the discrimination of neutral from adaptive genetic variation (Schmidt *et al.*, 2008a; Michel *et al.*, 2010).

The burst of genomics and transcriptomics now allows the study of the clinal variation of genome structure along geographic gradients, including the study of clinal variation in available annotated genes, transposable elements, inversions and speciation genes (Hohenlohe *et al.*, 2010; González *et al.*, 2010; Kolaczowski *et al.*, 2011; Wolf, Lindell & Backström, 2010; Nosil & Schluter, 2011; Rice *et al.*, 2011). Genomic studies suggest the existence of pervasive spatially varying selection acting at key genes throughout multiple genetic and metabolic pathways (Kolaczowski *et al.*, 2011; Hohenlohe *et al.*, 2010). For instance, genomic studies in latitudinal clines of *Drosophila melanogaster* have revealed the existence of pervasive adaptive variation in a wide number of genes coding for several key biological processes like cis-acting gene regulatory processes, transcription, chromatin regulation, circadian biology, development and body size growth (Kolaczowski *et al.*, 2011). Other studies suggest that this adaptive variation in fitness-associated loci has important effects on whole genome structure through diverse related processes (Nosil, Funk & Ortiz-Barrientos, 2009; Michel *et al.*, 2010). For instance, divergent selection also strongly influences the evolution of tightly and loosely linked neutral loci via linkage effects (gene hitchhiking). It also interacts with chromosomal inversion processes in diverse complex ways and facilitates genetic divergence. Finally, divergent selection can reduce gene flow and gene introgression from nearby populations, due to reduced fitness of immigrant genotypes, and therefore promotes genetic drift in neutral regions of the genome (Nosil, Funk & Ortiz-Barrientos, 2009; Michel *et al.*, 2010).

#### (5) Multivariate adaptive trait continuums

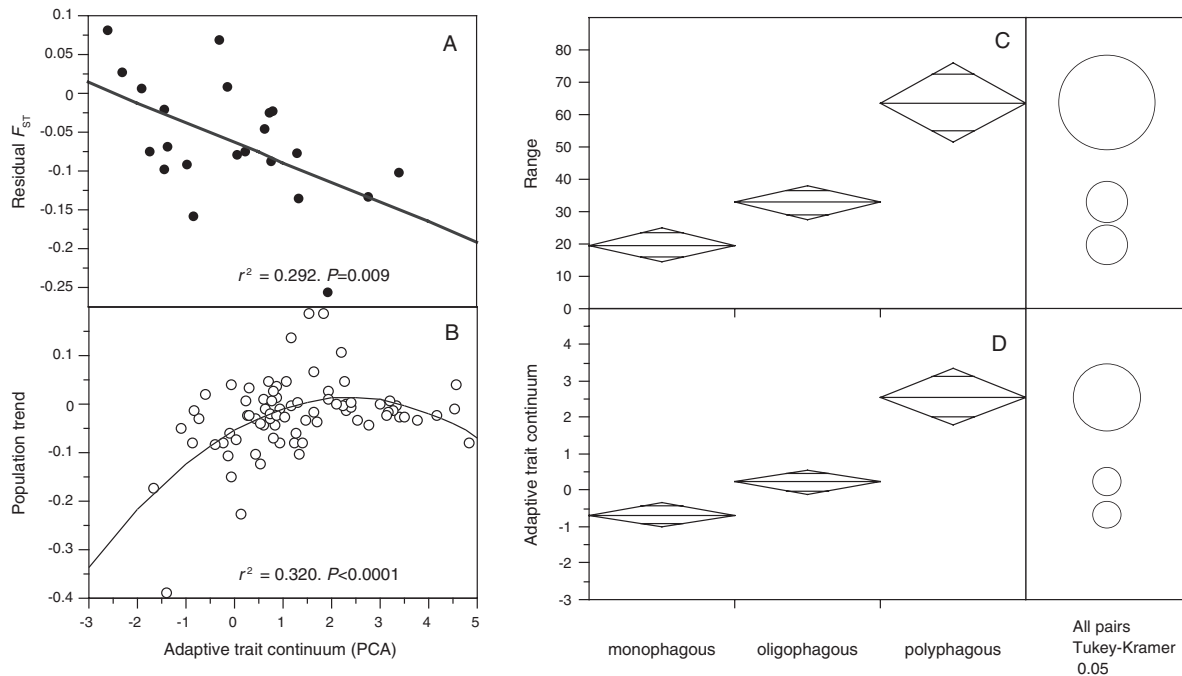
It has been shown recently that diverse adaptive traits and their interactions with the local environment influence the distribution of species along species richness gradients (e.g. Thuiller *et al.*, 2004; Stefanescu *et al.*, 2011a). Interestingly, some adaptive traits can be measured across many species allowing comparative approaches at the inter-specific level. These analyses have revealed the existence of suites of traits that tend to co-vary along a main axis of variation at the inter-specific level in plants (Grime *et al.*, 1997; Wright *et al.*, 2004; Chave *et al.*, 2009; Donovan *et al.*, 2011), mammals (Bielby *et al.*, 2007 and citations therein), birds (Sæther *et al.*, 2011), fishes (Jeschke & Kokko, 2009), phytoplankton (Litchman & Klausmeier, 2008), marine bacteria (Lauro *et al.*, 2009) and butterflies (Fig. 3). Adaptive trait continuums can be described easily and quantified using principal components analysis (PCA) or other ordination techniques (e.g. Wright *et al.*, 2004; Lauro *et al.*, 2009; Fig. 3). These continuums often range from specialized to more generalist species and/or from slow to fast lifestyles (Wright *et al.*, 2004; Bielby *et al.*, 2007; Sæther *et al.*, 2011; Fig. 3). The mechanistic origin of these taxon-specific trait continuums relies on the evolutionary emergence of contrasting life-history strategies that, in particular ecological contexts, maximize fitness by acquiring a different set of traits allowing for sustained population performance. Overall, adaptive trait continuums describe main axes of trait co-variation at the inter-specific level and quantify life-history variation and “phenotypic space” (*sensu* Donovan *et al.*, 2011).

Here we suggest that adaptive trait continuums may provide a useful mechanistic framework linking demography, gene flow and diversification dynamics along species richness gradients. For instance, an adaptive trait continuum is observed among 169 Mediterranean butterflies distributed along a regional species-richness gradient in Catalonia, Spain (Fig. 3; Stefanescu *et al.*, 2011a,b). For each species, we measured habitat thermal breadth, habitat aridity tolerance, dispersal capacity, host-plant diet breadth, and phenology (number of months with flight activity) (data from Stefanescu *et al.*, 2011a; see online supporting information, Appendix S1 for further details). A main inter-specific axis of variation across these traits accounted for 60% of the variation, ranging from specialist to generalist butterflies. The adaptive trait continuum (PCA scores) correlated with long-term demographic trends observed in the region (showing significantly higher declines in specialists, Fig. 3B) and, more generally, with observed differences in spatial genetic structure ( $F_{ST}$ , Fig. 3A). PCA scores of the adaptive trait continuum also co-varied with the distributional ranges of the species along the gradient (Fig. 3C), as illustrated for monophagous, oligophagous and polyphagous butterflies (Fig. 3D).

#### (6) Community context, adaptive behavioural traits, morphological divergence and speciation

Community context, i.e. the geographical variation in community composition and species interactions, can





**Fig. 3.** An example of the observed relationships between an adaptive trait continuum and (A)  $F_{ST}$  values reported for European butterflies (Nève, 2009), (B) long-term butterfly population trends in Catalonia (Stefanescu *et al.*, 2011a), and (C, D) species' distributional ranges in Catalonia, Spain. A principal components analysis (PCA) was performed between dispersal capacity, number of host-plant species used, phenology (number of weeks with flying activity per year), habitat temperature breadth and habitat aridity tolerance breadth for 169 butterfly species [data sources from Stefanescu *et al.* (2011a) and unpublished phenological data]. A main axis accounted for 60% of the variation in these traits and habitat variables (PCA variable). This PCA variable ranges from specialist lifestyles (monophagous with short phenology) to generalist lifestyles (polyphagous with wide phenology). The adaptive trait continuum correlates with the estimates of  $F_{ST}$  for European butterflies (values corrected for the spatial scale of each study extracting regression residuals between the spatial distance of the study and the reported  $F_{ST}$  values), the long-term population trends in Catalonia and the butterfly species ranges in Catalonia (number of transect routes on which the species was detected, see online supporting information, Appendix S1 for further details). Monophagous butterflies feed on plants of a single genus, oligophagous on plants of various genera from the same family, and polyphagous species on a diversity of plants belonging to various families. In C and D the line across the centre of each diamond represents the group mean. The vertical span of each diamond represents the 95% confidence interval for each group. Short horizontal lines near the top and bottom of each diamond are overlap marks at  $(\frac{\sqrt{2}}{2}) * CI$  above and below the group mean. Each pair of group means may be compared visually by examining how the comparison circles intersect. Circles for means that are significantly different do not intersect (Tukey-Kramer test,  $P < 0.0001$ ). Additional information is provided as online supporting information, Appendix S1.

influence the outcome of speciation and adaptive trait diversification processes (McPeck, 1996; Thompson, 2005; Abrams, 2006; Johnson & Stinchcombe, 2007; Carnicer, Abrams & Jordano, 2008a; Elias *et al.*, 2008; Schemske *et al.*, 2009). Therefore, a necessary step in order to understand fully the generation of species richness gradients is to elucidate which specific community contexts allowed increased diversification rates in each particular area and taxon. Empirical studies indicate that spatial and temporal variation in community context effectively cause geographical mosaics of selection, leading to morphological divergence and, in some cases, to speciation (Thompson, 2005). For instance, geographical differences in local community composition, such as the presence or absence of resource competitors, have been found to promote the emergence of morphologically distinct populations in crossbills (Benkman, Holimon & Smith, 2001; Parchman & Benkman, 2002; Benkman,

2003). These studies show that direct interactions among two community species (e.g. lodgepole pines and squirrels) can indirectly alter the nature of selection experienced by birds, and thus highlight the importance of community context in explaining diversification processes in adaptive morphological traits. Similarly, in butterflies, mutualistic interactions like Müllerian mimicry have been found to drive local adaptive trait variation with potential implications in diversification processes (Elias *et al.*, 2008).

Another aspect of community context that can facilitate morphological diversification is the uneven spatial and temporal distribution of resources (Price, 2008). For instance, fruits are predominantly confined to upper vegetation layers (Levey, 1988; Loiselle, 1988; Loiselle & Blake, 1991; Moles & Westoby, 2003; Moles *et al.*, 2004; Schleuning *et al.*, 2011) and invertebrate types and abundances differ strongly among adjacent vegetation types (Johnson *et al.*, 2005; Blondel *et al.*,



2006). Similarly, seasonality in resource variation is higher at upper vegetation layers but is usually less marked at the ground and understorey levels (Blondel, 1969; Poulin & Lefebvre, 1996). Empirical and theoretical evidence suggests that this uneven distribution of resources might promote ecological speciation through the evolutionary emergence of different feeding behavioural strategies with contrasting adaptive morphological traits (Feinsinger & Swarm, 1982; Smith *et al.*, 1997; Abrams, 2006; Carnicer *et al.*, 2008a; Carnicer, Jordano & Melián, 2009).

Finally, different community contexts can also induce changes directly on morphology through behavioural plastic responses (Agrawal, 2001; Price, Qvarnström & Irwin, 2003; Sol & Price, 2008). For example, some behavioural responses, such as resource switching behaviour, have been found to be pervasive and widespread in some bird communities (Fig. 4). Notably, different behavioural responses induced by community context are associated with morphological differences between bird species in adaptive traits (Fig. 4), providing some support for a role of community context and behavioural plasticity in bird morphological diversification and speciation processes (see Price *et al.*, 2003; Abrams, 2006; Sol & Price, 2008; Carnicer *et al.*, 2008a).

#### IV. EMERGING RESEARCH LINES AND TRENDS

In this section we briefly summarize a diverse suite of trait-based approaches in evolutionary ecology. These approaches may provide new tools and guidelines for future studies of species richness gradients.

(1) Genomics and transcriptomics may provide new ways to the study of the clinal variation of trade-offs between traits across gradients (Bochdanovits & de Jong, 2004; St-Cyr, Derome & Bernatchez, 2008), and may facilitate the study of genomic reaction norms and phenotypic plasticity across gradients (Gracey *et al.*, 2004; Aubin-Horth & Renn, 2009; Pfennig *et al.*, 2010). In addition, genome-scale models now enable the computation of phenotypic traits based on the genetic composition of the target organism (reviewed in Palsson, 2009).

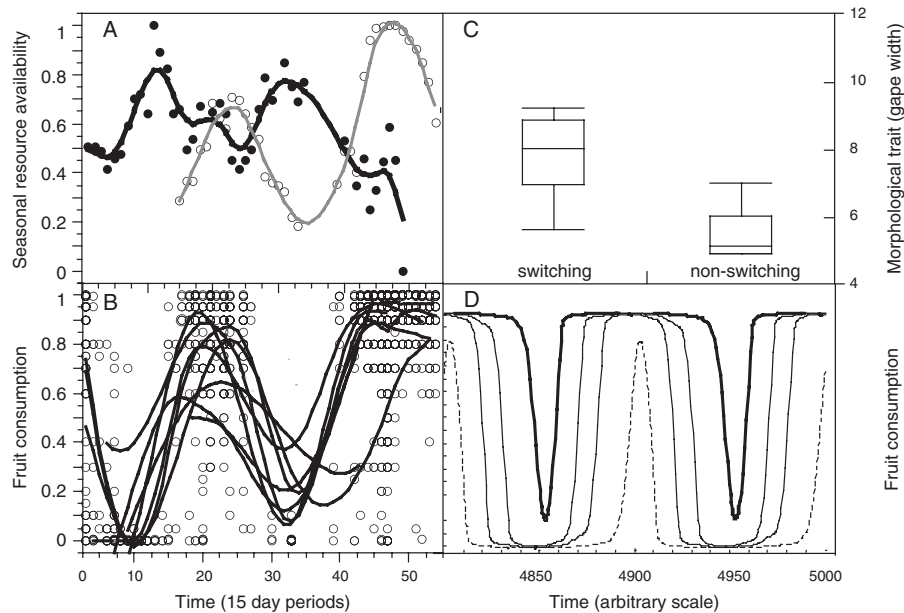
(2) The emerging field of comparative phylogenomics allows the analysis of the evolution of networks of regulatory genes related to specific adaptive traits (e.g. chemosensory systems determining host-plant choice and specialization in insects) (Tsong, Tuch & Johnson, 2006; Prud'homme, Gompel & Carrol, 2007; McBride & Arguello, 2007; Singh *et al.*, 2009; Pigliucci, 2010; Vieira & Rozas, 2011, Álvarez-Ponce, Aguadé & Rozas, 2011), and the analysis of the rise, spread, and death of gene families across phylogenies (Demuth & Hahn, 2009; Vieira & Rozas, 2011). All these approaches could be applied to the study of adaptive traits that influence speciation dynamics and the distribution of species across environmental gradients (e.g. Seehausen *et al.*, 2008; Kellermann *et al.*, 2009).

(3) The application of a diverse set of phylogenetic methods facilitates the study of the ecological and evolutionary

mechanisms implied in the genesis and maintenance of species richness gradients. For instance, new phylogenetic procedures are available to estimate trait-dependent speciation and extinction rates from incompletely resolved phylogenies (Fitzjohn, Maddison & Otto, 2009), perform hierarchic analyses of species richness gradients (Heard & Cox, 2007), assess time-for-speciation effects (Smith *et al.*, 2007; Kozak & Wiens, 2010; Wiens *et al.*, 2011); discern the effect of local competition and niche conservatism effects (Lovette & Hochachka, 2006), model trait evolution along phylogenies (Ree *et al.*, 2005; Ree, 2005; Paradis, 2005; Van Bocxlaer *et al.*, 2011), describe hybrid zones and phylogeographic breaks (Hewitt, 2001; Saetre *et al.*, 2001; Swenson & Howard, 2005), explore the relative roles of speciation and extinction rates in shaping diversification rates (Lovette, 2005; Weir, 2006; Weir & Schluter, 2007; Rabosky, 2010), test whether speciation is slowing down over time (Zink & Slowinski, 1995; Pybus & Harvey, 2000; Johnson & Cicero, 2004; Weir, 2006; Rabosky, 2009), assess differences in rates of diversification among clades (Barraclough & Nee, 2001; Cavender-Bares & Wilczek, 2003; Phillimore *et al.*, 2007; Wiens, 2007), assess differences in the rates of evolution of different traits or genes (Ackerly, 2009; Singh *et al.*, 2009), explore the role of trait evolution and assembly rules in structuring communities (Cavender-Bares & Wilczek, 2003; Ackerly *et al.*, 2006; Silvertown *et al.*, 2006; Lovette & Hochachka, 2006; Kraft *et al.*, 2007), analyze modes of geographical speciation (Barraclough & Vogler, 2000; Coyne & Price, 2000; Crisp *et al.*, 2009; Pigot *et al.*, 2010; Goldberg, Lancaster & Ree, 2011), quantify temporal variation in immigration and extinction rates in archipelagos (Ricklefs & Bermingham, 2001, 2004) and assess latitudinal divergences in diversification rates (Cardillo, 1999; Cardillo, Orme & Owens, 2005; Barraclough & Nee, 2001; Weir, 2006; Weir & Schluter, 2007; Rabosky, 2010; Kozak & Wiens, 2011).

(4) The identification of the genetic and developmental paths that control morphological traits and adaptive behaviours [“behavioural genes” *sensu* Fitzpatrick *et al.*, (2005)] provides a new tool to study diversification processes. For example, some pioneering works have identified some genes and developmental paths of traits putatively implied in bird speciation processes. These genes and metabolic paths are possibly shared by most bird species and might become a powerful tool for the comparative study of morphological diversification (Wu *et al.*, 2004; Abzhanov *et al.*, 2004, 2006; Fitzpatrick *et al.*, 2005, Campàs *et al.*, 2010; Mallarino *et al.*, 2011).

(5) Studying dispersal and movement behaviour along species richness gradients is likely to become more feasible with advances in molecular techniques and tracking technology and the application of recently developed theoretical frameworks (Bowler & Benton, 2005; Holyoak *et al.*, 2008; Nathan *et al.*, 2008; Revilla & Wiegand, 2008; Clobert *et al.*, 2009; Hanski & Mononen, 2011; Wheat *et al.*, 2011). Future studies should highlight how individual movements and spatial population dynamics influence altitudinal and latitudinal species richness gradients.



**Fig. 4.** An example of the possible role of adaptive switching behaviour in promoting morphological diversification of foraging traits. Bird communities are often characterized by seasonal variation in resource supply. Birds respond to seasonal resource fluctuations with behaviourally plastic responses. Here we show an example of a Mediterranean bird community located in South-western Spain. (A) Black dots illustrate the seasonal variation in insect abundance in a Mediterranean shrubland over two years. White dots represent the seasonal variation in fruit abundance. The resources present alternate peaks, with spring peaks of insects and fruits peaking in autumn. (B) Observed behavioural responses of the birds switching in response to seasonal variation in resource supply. Each line represents a different species. Each dot represents a fecal sample in which the percentage of fruits and insects in the diet was measured. The bulk of these species switch between resources matching the seasonal fluctuations in resource supply. Species differ in the speed of switching responses, presenting rapid and delayed switching responses to resource fluctuation. Some species behave as specialists in one of the two resource channels. Delayed switchers and specialists are not shown. (C) Differences in behaviour are associated with morphological differences in foraging traits. Switching species have wider gapes than specialists. The line across the middle of the box identifies the median sample value. The ends of the box are the 25th and 75th quantiles. (D) Recent theoretical models (Abrams, 2006) demonstrate that behavioural switching between two food types in a variable environment promotes coexistence and evolutionary diversification of foraging adaptive traits of competing species. Diversification is caused by disruptive selection of a morphological foraging trait that is related to the relative use of two food types or resource channels. The figure illustrates the theoretical expected switching behavioural dynamics of the evolutionarily stable coalition for four generalist species derived from the Abrams (2006) model. Full details of the simulation are provided as online supporting information (Appendix S2); see Abrams (2006) and Carnicer *et al.* (2008a) for an explanation and analysis of the model.

(6) The empirical study of behavioural dynamics on target species along environmental gradients (e.g. Snell-Rood & Badyaev, 2008) should be accompanied by the empirical estimation of demographic parameters (dispersal, survival, fecundity, population variability) (Zang, 1980; Badyaev & Ghalambor, 2001; Sæther *et al.*, 2008, 2011) and habitat quality measures (*sensu* Johnson, 2007). Community-wide evaluations of plastic behavioural responses (e.g. Carnicer *et al.*, 2008a, 2009) are required to evaluate the role of behaviour on diversification dynamics and to assess the geographical variation of adaptive behaviours along environmental gradients (Jetz & Rubenstein, 2011).

(7) The seasonal distribution of resource availability has been identified as a major cause of the evolutionary origin of migration (Salewski & Bruderer, 2007; Boyle, 2008), a behavioural adaptive trait that strongly influences the shape and temporal variation of species richness gradients (Hurlbert & Haskell, 2003; Carnicer & Díaz-Delgado, 2008).

More detailed and extensive empirical studies addressing the spatial and seasonal variation of resources along species richness gradients are needed (Hurlbert & Haskell, 2003; Buler, Moore & Woltmann, 2007; Peters *et al.* 2010). Seasonal patterns of resource variation are linked to migration movements, life-history evolution and may also drive diversification dynamics at longer temporal scales (Johnson *et al.*, 2005; Novotny *et al.*, 2007; Buler *et al.*, 2007; Boyle & Conway, 2007; Price, 2008; Carnicer *et al.*, 2008a, 2009; Boyle, 2008). Some pioneering studies are starting to describe global patterns in resource seasonality (Ting *et al.*, 2008). Interestingly enough, global patterns in seasonality of fruit resources are correlated with measures of actual evapotranspiration (Ting *et al.*, 2008), and other global predictors of species richness gradients like temperature (Hawkins *et al.*, 2003a, b).

(8) An increasing number of theoretical models also provide insights into the evolutionary and ecological processes

that mould species richness gradients (Tables 2, 3), like diversification dynamics (Dieckmann & Doebeli, 1999; Hubbell, 2001; Case & Taper, 2000; Doebeli & Dieckmann, 2003; Gavrillets & Vose, 2005; Abrams, 2006; Roy & Goldberg, 2007; Rangel, Diniz-Filho & Colwell, 2007; Bolnick & Fitzpatrick, 2007; Arita & Vázquez-Dominguez, 2008; Carnicer *et al.*, 2008a; van Doorn, Edelaar & Weissing, 2009; Heinz *et al.*, 2009; Gavrillets & Losos, 2009; Faria & Navarro, 2010; Rosindell & Phillimore, 2011) and other complementary processes like dispersal limitation, niche filtering and demographic stochasticity (Hubbell, 2001; Rangel & Diniz-Filho, 2005; Rangel *et al.*, 2007; Hugueny, Cornell & Harrison, 2007; Kadmon & Allouche, 2007; Rosindell & Phillimore, 2011), habitat selection (Fretwell & Lucas, 1970; Morris, 2003; Fletcher, 2006) or gene-flow in metacommunities (Urban & Skelly, 2006; Urban *et al.*, 2008).

## V. CONCLUSIONS

(1) Species characterized by more specialized adaptive traits show spatially nested distributions along species richness gradients (Fig. 2) (Carnicer *et al.*, 2008a; Stefanescu *et al.*, 2011a; Alexander *et al.*, 2011). Rare species also show higher effects of demographic stochasticity, asynchronous and more isolated population dynamics, low dispersal fluxes and greater spatial genetic variation. By contrast, widespread generalists often show more synchronous spatial population dynamics, demographically track environmental variation and resource peaks, experience lower effects of demographic stochasticity, attain higher population sizes, and are characterized by lower spatial genetic variation (Sæther *et al.*, 2011; Fig. 3). Demographic dynamics differ greatly between species located at opposite extremes of adaptive trait continuums (Sæther *et al.*, 2011; Shultz *et al.*, 2005; Fig. 3). Adaptive trait continuums usually range from fast to slow and/or from specialist to generalist lifestyles.

(2) More empirical studies quantifying the effects of environmental conditions on the deterministic and stochastic components of population dynamics along latitudinal and altitudinal species richness gradients are required (e.g. Sæther *et al.*, 2003, 2008, 2011). These studies should provide a better description of the geographic mosaics in population dynamics that are associated with the maintenance of species richness gradients (Table 2).

(3) A related issue is the study of the geography of colonization and extinction rates along species richness gradients. Recent studies have found geographic differences in extinction rates along regional species richness gradients (e.g. Carnicer *et al.*, 2007, 2008b; Fig. 2). Greater extinction rates in specialists are frequently observed (Kotiaho *et al.*, 2005; Shultz *et al.*, 2005). However, more studies are required to achieve a precise knowledge of which adaptive traits and behaviours are moulding demographic and dispersal rates (e.g. Sæther *et al.*, 2003, 2008, 2011; Brotons, Pons & Herrando, 2005; Sirami, Brotons & Martin, 2008).

(4) Empirical evidence suggests that adaptive traits associated with thermal tolerance, resource use, phenology and dispersal capacity play a significant role on setting the limits of species' distributions along altitudinal and latitudinal gradients. Complementary studies also assert that other life-history traits (e.g. lifespan, fecundity, survival, body size) frequently interact with phenology, dispersal and thermal-tolerance traits across latitudinal and regional clines (Schmidt & Paaby, 2008; Klemme & Hanski, 2009; Paaby *et al.*, 2010; Kolaczowski *et al.*, 2011). Future studies dealing with species richness gradients should explicitly consider phenological and behavioural schedules (e.g. insect voltinism and diapause cycles; plant and animal annual cycles) and plastic adaptive behaviours (e.g. behavioural barriers to dispersal, condition-dependent dispersal).

(5) Several studies highlight that functional groups characterized by different suites of adaptive traits are differentially distributed across species richness gradients (Carnicer & Díaz-Delgado, 2008; Stefanescu *et al.*, 2011a; Kissling, Sekercioglu & Jetz, 2011; Lennon *et al.*, 2011; Ekross & Kuussaari, 2011; Alexander *et al.*, 2011). Therefore, the identification and separate study of functional groups facilitates the ecological interpretation of species richness gradients (Carnicer & Díaz-Delgado, 2008; Kissling, Böhning-Gaese & Jetz, 2009). Similarly, quantifying and mapping trait variation across geographic gradients warrants further scientific effort (Reich, Walters & Ellsworth, 1997; De Jong & Bochdanovits, 2003; Reich & Oleksyn, 2004; Sørensen *et al.*, 2005; Kyriacou *et al.*, 2008; Jetz, Sekercioglu & Böhning-Gaese, 2008; Jetz & Rubenstein, 2011).

(6) Adaptive trait continuums may provide a powerful mechanistic framework to: (1) analyze life-history variation across species-richness gradients, (2) explore correlates with demography and gene flow estimates, and (3) to explain inter-specific differences in long-term diversification trends. Improved descriptions of inter-specific trait continuums may be achieved by integrating data at several hierarchical levels (genome, transcriptome, proteome, metabolome, interactome, regulome, fluxome, phenome, environmental and demographic data) using available high-throughput technologies (e.g. Lauro *et al.*, 2009; Macel, Van Dam & Keurentjes, 2010; Houle, Govindaraju & Omholt, 2010; Raes *et al.*, 2011).

(7) Mechanistic approaches linking genotype, phenotype, organism performance and fitness are becoming available for some adaptive traits that limit species distributions (Dalziel *et al.*, 2009; Dillon *et al.*, 2009; Storz & Wheat, 2010). These mechanistic approaches are also becoming available for traits involved in reproductive isolation and speciation processes along gradients (Seehausen *et al.*, 2008; Rice *et al.*, 2011). Generally, the analysis of integrated mechanistic approaches is currently facilitated by the parallel burst of genomics, transcriptomics, metabolomics, metagenomics and phenomics (Palsson, 2009; Macel *et al.*, 2010; Houle *et al.*, 2010). Indeed, new studies are using 'omic' techniques to study clinal variation of adaptive traits and genetic markers across latitudinal, altitudinal and regional environmental gradients (Michel



*et al.*, 2010; González *et al.*, 2010; Kolaczowski *et al.*, 2011; Raes *et al.*, 2011; Gianoulis *et al.*, 2009; see Section IV). These studies report pervasive adaptive clinal variation related to a great variety of biological processes and molecular markers (Michel *et al.*, 2010; Hohenlohe *et al.*, 2010; Kolaczowski *et al.*, 2011).

(8) Several researchers have pointed out that the explicit consideration of adaptive traits and plastic behaviours can profoundly change the behaviour of theoretical models (e.g. Reed & Levine, 2005; Fletcher, 2006; Abrams, 2006). For instance, recent theoretical works (Kondoh, 2003; Abrams, 2006; Rueffler, Van Dooren & Metz, 2007; van Doorn *et al.*, 2009; Pfennig *et al.*, 2010; Snell-Rood *et al.*, 2010; Moczek *et al.*, 2011) highlight the importance of adaptive behaviours and phenotypic plasticity on diversification and population interaction dynamics. Models of clinal speciation explicitly simulate the evolution of traits and diversification processes across environmental gradients (Doebeli & Dieckmann, 2003; Heinz *et al.*, 2009). Similarly, fitness-based models that explicitly incorporate adaptive traits and phenology have been successfully applied to predict species' distributions (Kearney & Porter, 2009; Chuine, 2010).

(9) Clade-specific studies of the sequential evolution of adaptive traits along phylogenies and their relationship with diversification rates are improving our current understanding of adaptive radiations, diversification processes and the history of clade migrations (Böhning-Gaese *et al.*, 2003; Davies *et al.*, 2004; Freckleton & Harvey, 2006; Wiens, 2007; Menken *et al.*, 2009; Hodges & Derieg, 2009; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010; Section IV).

(10) To assess effectively the importance of community context in driving diversification processes new research should be conducted in several areas: (1) the study of the spatial and temporal variation of community context (i.e. consumer-resource interaction networks) along geographical gradients of species richness (Callaway *et al.*, 2002; Olesen & Jordano, 2002; Schemske *et al.*, 2009; Carnicer *et al.*, 2009; Moya-Laraño, 2010; McKinnon *et al.*, 2010; Rasmann & Agrawal, 2011), (2) the quantitative study of the spatial and temporal variation of resource distribution along species richness gradients (Johnson *et al.*, 2005; Novotny *et al.*, 2007; Ting, Hartley & Burns, 2008), and (3) the comparative examination of phenotypically plastic responses along species richness gradients (Smith *et al.*, 1997; Price *et al.*, 2003; Sol & Price, 2008; Abrams, 2006; Carnicer *et al.*, 2008a; Aubin-Horth & Renn, 2009; Pfennig *et al.*, 2010; Snell-Rood *et al.*, 2010; Moczek *et al.*, 2011).

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## VII. REFERENCES

- ABRAMS, P. A. (2006). The effects of switching behaviour on the evolutionary diversification of generalist consumers. *American Naturalist* **168**, 645–659.
- ABZHANOV, A., KUO, W. P., HARTMANN, C., GRANT, B. R., GRANT, P. R. & TABIN, C. J. (2006). The calmodulin pathway and evolution of elongated beak morphology in Darwin's finches. *Nature* **442**, 563–567.
- ABZHANOV, A., PROTAS, M., GRANT, B. R., GRANT, P. R. & TABIN, C. J. (2004). Bmp4 and morphological variation of beaks in Darwin's finches. *Science* **305**, 1462–1464.
- ACKERLY, D. D. (2009). Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19631–19636.
- ACKERLY, D. D., SCHWILK, D. W. & WEBB, C. O. (2006). Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology* **87**, S50–S61.
- AGRAWAL, A. A. (2001). Phenotypic plasticity in the interactions and the evolution of species. *Science* **294**, 321–326.
- ALEXANDER, J. M., KUEFFER, C., DAEHLER, C. C., EDWARDS, P. J., PAUCHARD, A., SEIPEL, T. & MIREN, C. (2011). Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 656–661.
- ÁLVAREZ-PONCE, D., AGUADÉ, M. & ROZAS, J. (2011). Comparative genomics of the vertebrate insulin/TOR signal transduction pathway: A network-level analysis of selective pressures. *Genome Biology and Evolution* **3**, 87–101.
- ANGILLETTA, M. J., WILSON, R. S., NAVAS, C. & JAMES, R. S. (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology and Evolution* **18**, 234–240.
- ARITA, H. T. & VÁZQUEZ-DOMÍNGUEZ, E. (2008). The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. *Ecology Letters* **11**, 1–11.
- ARNOLD, S. J. (1983). Morphology, performance and fitness. *American Zoologist* **23**, 347–361.
- ATAURI, J. A. & DE LUCIO, J. V. (2001). The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. *Landscape Ecology* **16**, 147–159.
- AUBIN-HORTH, N. & RENN, S. C. P. (2009). Genomic reaction norms: using integrative biology to understand molecular mechanisms of phenotypic plasticity. *Molecular Ecology* **18**, 3763–3780.
- BACKSTRÖM, N., LINDELL, J., ZHANG, Y., PALKOPOULOU, E., QVARNSTRÖM, A., SAETRE, G. P. & ELLEGREN, H. (2010). A high-density scan of the Z chromosome in *Ficedula* flycatchers reveals candidate loci for diversifying selection. *Evolution* **64**, 3461–3475.
- BADYAEV, A. V. & GHALAMBOR, C. K. (2001). Evolution of life stories along elevational gradients: trade-off between parental care and fecundity in birds. *Ecology* **82**, 2948–2960.
- BAGUETTE, N., CLOBERT, J. & SHTICKZELLE, N. (2011). Metapopulation dynamics of the bog fritillary butterfly: experimental changes in habitat quality induced negative density-dependent dispersal. *Ecography* **34**, 170–176.
- BARRACLOUGH, T. G. & NEE, S. (2001). Phylogenetics and speciation. *Trends in Ecology and Evolution* **16**, 391–399.
- BARRACLOUGH, T. G. & VOGLER, A. P. (2000). Detecting the geographical pattern of speciation from species-level phylogenies. *American Naturalist* **155**, 419–434.
- BAXTER, S. W., NADEAU, N. J., MAROJA, L. S., WILKINSON, P., COUTERMAN, B. A., DAWSON, A., BELTRAN, M., PEREZ-ESPONA, S., CHAMBERLAIN, N., FERGUSON, L., CLARK, R., DAVIDSON, C., GLITHERO, R., MALLET, J., OWEN MCMILLAN, W., KRONFORST, M., JORON, M., FRENCH-CONSTANT, R. H., JIGGINS, C. D. (2010). Genomic hotspots for adaptation: the population genetics of Müllerian mimicry in the *Heliconius melpomene* clade. *PLoS Genetics* **6**, e1000794.
- BELLIURE, J., SORCI, J., MÖLLER, A. P. & CLOBERT, J. (2000). Dispersal distance predicts subspecies richness in birds. *Journal of Evolutionary Ecology* **13**, 480–487.

- BENKMAN, C. W. (2003). Divergent selection drives the adaptive radiation of crossbills. *Evolution* **57**, 1176–1181.
- BENKMAN, C. W., HOLLMON, W. C. & SMITH, J. W. (2001). The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. *Evolution* **55**, 282–294.
- BENTON, M. J. & EMERSON, B. C. (2007). How did life become so diverse? The dynamics of diversification according to the fossil record and molecular phylogenetics. *Palaeontology* **50**, 23–40.
- BERNARDO, J., OSSOLA, R., SPOTILA, J. & CRANDALL, K. A. (2007). Interspecific physiological variation as a tool for cross-species assessments of global warming-induced endangerment: validation of an intrinsic determinant of macroecological and phylogenetic structure. *Biology Letters* **3**, 695–699.
- BIELBY, J., MACE, G. M., BININDA-EMONDS, O. R. P., CARDILLO, M., GITTLEMAN, J. L., JONES, K. E., ORME, C. D. & PURVIS, A. (2007). The fast-slow continuum in mammalian life-history: an empirical reevaluation. *American Naturalist* **169**, 748–757.
- BLACKMAN, B. K. (2010). Connecting genetic variation to phenotypic clines. *Molecular Ecology* **19**, 621–623.
- BLONDEL, J. (1969). *Synécologie des Passereaux Résidents et Migrateurs dans le Midi Méditerranéen Français*. Centre Regional de Documentation Pédagogique.
- BLONDEL, J., THOMAS, D. W., CHARMANTIER, A., PERRET, P., BOURGAULT, P. & LAMBRECHTS, M. M. (2006). A thirty-year study of phenotypic and genetic variation of Blue Tits in Mediterranean habitat mosaics. *BioScience* **56**, 661–673.
- BOCHDANOVITS, Z. & DE JONG, G. (2004). Antagonistic pleiotropy for life-history traits at the gene expression level. *Proceedings of the Royal Society of London Series B* **271**, S75–S78.
- BOCK, C. E. & JONES, Z. F. (2004). Avian habitat evaluation: should birds count? *Frontiers in the Ecology and the Environment* **2**, 403–410.
- BÖHNING-GAESE, K., CAPRANO, T., VAN EWIJK, K. & VEITH, M. (2006). Range size: disentangling current traits and phylogenetic and biogeographic factors. *American Naturalist* **167**, 555–567.
- BÖHNING-GAESE, K., GONZÁLEZ-GUZMÁN, L. I. & BROWN, J. H. (1998). Constraints on dispersal and the evolution of the avifauna of the Northern Hemisphere. *Evolutionary Ecology* **12**, 767–783.
- BÖHNING-GAESE, K. & OBERATH, R. (1999). Phylogenetic effects on morphological, life-history, behavioural and ecological traits in birds. *Evolutionary Ecological Research* **1**, 347–364.
- BÖHNING-GAESE, K., SCHUDA, M. D. & HELBIG, A. J. (2003). Weak phylogenetic effects on ecological niches of *Sylvia* warblers. *Journal of Evolutionary Biology* **16**, 956–965.
- BOLKER, B., HOLYOAK, M., KRIVAN, V., ROWE, L. & SCHMITZ, O. (2003). Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology* **84**, 1101–1114.
- BOLNICK, D. I. & FITZPATRICK, B. (2007). Sympatric speciation: theory and empirical data. *Annual Review of Ecology Evolution and Systematics* **38**, 459–487.
- BOMBLIES, K. & WEIGEL, D. (2010). *Arabidopsis* and relatives as models for the study of genetic and genomic incompatibilities. *Philosophical Transactions of the Royal Society B* **365**, 1815–1823.
- BOWLER, D. E. & BENTON, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* **80**, 205–225.
- BOULINIER, T., NICHOLS, J. D., HINES, J. E., SAUER, J. R., FLATHER, C. H. & POLLOCK, C. H. (1998). Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America* **95**, 7497–7501.
- BOYLE, W. A. (2008). Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. *Journal of Animal Ecology* **77**, 1122–1128.
- BOYLE, W. A. & CONWAY, C. J. (2007). Why migrate? A test of the evolutionary precursor hypothesis. *American Naturalist* **169**, 344–359.
- BRADSHAW, H. D. & SCHEMSKE, D. W. (2003). Allele substitution at a flower color locus produces a pollinator shift in two monkeyflower species (*Mimulus*). *Nature* **426**, 176–178.
- BRÄNDLE, M., PRINZING, A., PFEIFER, R. & BRANDL, R. (2002). Dietary niche breadth for central European birds: correlations with species-specific traits. *Evolutionary Ecology Research* **4**, 643–657.
- BROTNS, L., PONS, P. & HERRANDO, S. (2005). Colonisation of dynamic Mediterranean landscapes: where do birds come from after fire? *Journal of Biogeography* **32**, 789–798.
- BROWN, J. H. (1981). Two decades of Homage to Santa Rosalia: Toward a general Theory of Diversity. *American Zoologist* **21**, 877–888.
- BULER, J. J., MOORE, F. R. & WOLTMANN, S. (2007). A multi-scale examination of stopover habitat use by birds. *Ecology* **88**, 1789–1802.
- BURNS, K., HACKETT, S. J. & KLEIN, N. K. (2003). Phylogenetic relationships of Neotropical honeycreepers and the evolution of feeding morphology. *Journal of Avian Biology* **34**, 360–370.
- CALLAWAY, R. M., BROOKER, R. W., CHOLER, P., KIKVIDZE, Z., LORTIE, C. J., MICHALET, R., PAOLINI, L., PUGNAIRE, F. I., COOK, B. J., ASCHEHOUG, E. T., ARMAS, C. & NEWINGHAM, B. (2002). Positive interactions among alpine plants increases with stress: a global experiment. *Nature* **417**, 844–848.
- CAMPÀS, O., MALLARINO, R., HERREL, A., BRENNER, M. P. & ABZHANOV, A. (2010). Scaling and shear transformations capture beak shape variation in Darwin's finches. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 3356–3360.
- CARDILLO, M. (1999). Latitude and rates of diversification in birds and butterflies. *Proceedings of the Royal Society of London Series B-Biological Sciences* **266**, 1221–1226.
- CARDILLO, M., ORME, C. D. L. & OWENS, I. P. F. (2005). Testing for latitudinal bias in diversification rates: a example using New World birds. *Ecology* **86**, 2278–2287.
- CARNICER, J., ABRAMS, P. A. & JORDANO, P. (2008a). Switching behaviour and diversification: empirical community-wide evidence matches theoretical predictions. *Ecology Letters* **11**, 802–808.
- CARNICER, J., BROTONS, L., SOL, D. & DE CÁCERES, M. (2008b). Random sampling, abundance-extinction dynamics and niche-filtering immigration constraints explain the generation of species richness gradients. *Global Ecology and Biogeography* **17**, 352–362.
- CARNICER, J., BROTONS, L., SOL, D. & JORDANO, P. (2007). Community based processes behind species richness gradients: contrasting abundance-extinction dynamics and sampling effects in low- and high productivity areas. *Global Ecology and Biogeography* **16**, 709–719.
- CARNICER, J. & DÍAZ-DELGADO, R. (2008). Geographic differences between functional groups in patterns of bird species richness gradients in North America. *Acta Oecologica* **33**, 253–264.
- CARNICER, J., JORDANO, P. & MELIÁN, C. J. (2009). The temporal dynamics of resource use by frugivorous birds: a network approach. *Ecology* **90**, 1958–1970.
- CARRASCAL, L. M., VILLÉN-PÉREZ, S. & SEOANE, J. (2011). Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods. *Ecological Research*, on line early view.
- CASE, T. J. & TAPER, M. L. (2000). Interspecific competition, environmental gradients, gene flow and the coevolution of species' borders. *American Naturalist* **155**, 583–605.
- CAVENDER-BARES, J. & WILCZEK, A. (2003). Integrating micro- and macroevolutionary processes in community ecology. *Ecology* **84**, 592–597.
- CHAMBERLAIN, N. L., HILL, R. I., KAPAN, D. D., GILBERT, L. E. & KRONFORST, M. R. (2009). Polymorphic butterfly reveals the missing link in ecological speciation. *Science* **326**, 847–850.
- CHAVE, J., COOMES, D., JANSEN, S., LEWIS, S. L., SWENSON, N. G. & ZANNE, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.
- CHUINE, I. (2010). Why does phenology drive species distribution?. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 3149–3160.
- 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.
- COLEMAN, B. D., MARES, M. A., WILLIG, M. R. & HSIEH, Y. (1982). Randomness, area, and species richness. *Ecology* **63**, 1121–1133.
- COLLINGE, J. E., ANDERSON, A. R., WEEKS, A. R., JOHNSON, T. K. & MCKECHNIE, S. W. (2008). Latitudinal and cold-tolerance variation associate with DNA repeat-number variation in the hsr-omega RNA gene of *Drosophila melanogaster*. *Heredity* **101**, 260–270.
- COULSON, T., BENTON, T. G., DALL, S. R. X. & KENDALL, B. E. (2006). Putting evolutionary biology back in the ecological theatre: a demographic framework mapping genes to communities. *Evolutionary Ecology Research* **8**, 1155–1171.
- COYNE, J. A. & PRICE, T. D. (2000). Little evidence for sympatric speciation in island birds. *Evolution* **54**, 2166–2171.
- CRISP, M. D., ARROYO, M. T. K., COOK, L. G., GANDOLFO, M. A., JORDAN, G. J., MCGLONE, M. S., WESTON, P. H., WESTOBY, M., WILF, P. & LINDER, H. P. (2009). Phylogenetic biome conservatism on a global scale. *Nature* **458**, 754–756.
- CURRIE, D. J. (1991). Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist* **137**, 27–49.
- CURRIE, D. J., MITTELBACH, G. G., CORNELL, H. V., FIELD, R., GUÉGAN, J. F., HAWKINS, B. A., KAUFMANN, D. M., KERR, J. T., OBERDORFF, T., O'BRIEN, E. & TURNER, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* **7**, 1121–1134.
- DALL, S. R. X., GIRALDEAU, L.-A., OLSSON, O., MCNAMARA, J. M. & STEPHENS, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution* **20**, 187–193.
- DALZIEL, A. C., ROGERS, S. M. & SCHULTE, P. M. (2009). Linking genotypes to phenotypes and fitness: how mechanistic biology can inform molecular ecology. *Molecular Ecology* **18**, 4997–5017.
- DANCHIN, É., GIRALDEAU, L.-A., VALONE, T. J. & WAGNER, R. H. (2004). Public information: from noisy neighbours to cultural evolution. *Science* **305**, 487–491.
- DAVIES, J., BARRACLOUGH, T. G., SAVOLAINEN, V. & CHASE, M. W. (2004). Environmental causes for plant diversity gradients. *Philosophical Transactions of the Royal Society of London B-Biological Sciences* **359**, 1645–1656.
- DE JONG, G. & BOCHDANOVITS, Z. (2003). Latitudinal clines in *Drosophila melanogaster*: body size, allozyme frequencies, inversion frequencies, and the insulin-signalling pathway. *Journal of Genetics* **82**, 207–223.
- DEMUTH, J. P. & HAHN, M. W. (2009). The life and death of gene families. *Bioessays* **31**, 29–39.



- DE QUEIROZ, A. (2002). Contingent predictability in evolution: key traits and diversification. *Systematic Biology* **51**, 917–929.
- DESROCHERS, A. & DIAMOND, J. M. (1986). Evolution of ecological segregation in the New Guinea montane avifauna. In: *Community Ecology* (eds J. M. DIAMOND and T. J. CASE) pp. 98–125. Harper and Row, New York, USA.
- DESROCHERS, A. & HANNON, S. (1997). Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* **4**, 1204–1210.
- DIECKMANN, U. & DOEBELI, M. (1999). On the origin of species by sympatric speciation. *Nature* **400**, 354–357.
- DILLON, M. E., WANG, G., GARRITY, P. A. & HUEY, R. B. (2009). Thermal preference in *Drosophila*. *Journal of Thermal Biology* **34**, 109–119.
- DOEBELI, M. & DIECKMANN, U. (2003). Speciation along environmental gradients. *Nature* **421**, 259–264.
- DOLIGEZ, B., CADET, C., DANCHIN, E. & BOULINIER, T. (2003). When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* **66**, 973–998.
- DOLIGEZ, B., DANCHIN, E. & CLOBERT, J. (2002). Public information and breeding habitat selection in a wild bird population. *Science* **297**, 1168–1170.
- DONOGHUE, M. J. (2005). Key innovations, convergence, and success: macroevolutionary lessons from plant phylogeny. *Palaeobiology* **31**, 77–93.
- DONOVAN, L. A., MAHERALI, H., CARUSO, C. M., HUBER, H. & DE KROON, H. (2011). The evolution of the worldwide leaf economics spectrum. *Trends in Ecology and Evolution* **26**, 88–95.
- DYER, L. A., SINGER, M. S., LILL, J. T., STIREMAN, J. O., GENTRY, G. L., MARQUIS, R. J., RICKLEFS, R. E., GREENEY, H. F., WAGNER, D. L., MORAIS, H. C., DINIZ, I. R., KURSAR, T. A. & COLEY, P. D. (2007). Host specificity of Lepidoptera in tropical and temperate forests. *Nature* **448**, 696–699.
- EDWARDS, S. V., KINGAN, S. B., CALKINS, J. D., BALAKRISHNAN, C. N., JENNINGS, W. B., SWANSON, W. J. & SORENSON, M. D. (2005). Speciation in birds: genes, geography, and sexual selection. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 6550–6557.
- EKKROOS, J. & KUUSSAARI, M. (2011). Landscape context affects the relationship between local and landscape species richness of butterflies in semi-natural habitats. *Ecography*, on line early view.
- ELIAS, M., GOMPERT, Z., JIGGINS, C. & WILLMOTT, K. (2008). Mutualistic interactions drive ecological niche convergence in a diverse butterfly community. *Plos Biology* **6**, e300.
- ELLEGREN, H. & SHELDON, C. (2008). Genetic basis of fitness differences in natural populations. *Nature* **452**, 169–175.
- ERICSON, G. P., IRESTDOT, M. & JOHANSSON, U. S. (2003). Evolution, biogeography, and patterns of diversification in passerine birds. *Journal of Avian Biology* **34**, 3–15.
- EVANS, K. L., GREENWOOD, J. J. D. & GASTON, K. J. (2005a). The roles of extinction and colonization in generating species-energy relationships. *Journal of Animal Ecology* **74**, 498–507.
- EVANS, K. L., JAMES, N. A. & GASTON, K. J. (2006). Abundance, species richness and energy availability in the North American avifauna. *Global Ecology and Biogeography* **15**, 372–385.
- EVANS, K. L., WARREN, P. H. & GASTON, K. J. (2005b). Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews* **80**, 1–25.
- FARIA, R. & NAVARRO, A. (2010). Chromosomal speciation revisited: rearranging theory with pieces of evidence. *Trends in Ecology and Evolution* **25**, 660–669.
- FEINSINGER, P. & SWARM, L. A. (1982). Ecological release, seasonal variation in food supply, and the hummingbird *Amazilia tobaci* on Trinidad and Tobago. *Ecology* **63**, 1574–1587.
- FINE, P. V. & REE, R. H. (2006). Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *American Naturalist* **168**, 796–804.
- FITZJOHN, R. G., MADDISON, W. P. & OTTO, S. P. (2009). Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology* **58**, 595–611.
- FITZPATRICK, M. J., BENS SHAHAR, Y., SMID, H. M., VET, L. E. M., ROBINSON, G. E. & SKOŁOWSKI, M. B. (2005). Candidate genes for behavioural ecology. *Trends in Ecology and Evolution* **20**, 97–104.
- FJELDSA, J. & RAHBEK, C. (2006). Diversification of tanagers, a species rich group, from lowlands to montane regions of South America. *Integrative and Comparative Biology* **46**, 72–81.
- FLETCHER, R. J. (2006). Emergent properties of conspecific attraction in fragmented landscapes. *American Naturalist* **168**, 207–219.
- FLETCHER, R. J. (2007). Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology* **76**, 598–606.
- FLOWERS, J. M., HANZAWA, Y., HALL, M. C., MOORE, R. C., PURUGGANAN, M. D. (2009). Population genomics of the *Arabidopsis thaliana* flowering time gene network. *Molecular Biology and Evolution* **26**, 2475–2488.
- FORSMAN, J. T., HJERNQUIST, M. B., TAIPALE, J. & GUSTAFSSON, L. (2008). Competitor density cues for habitat quality facilitating habitat selection and investment decisions. *Animal Behaviour* **19**, 539–545.
- FORSMAN, J. T. & MÖNKKÖNEN, M. (2003). The role of climate in limiting resident bird populations. *Journal of Biogeography* **30**, 55–70.
- FRECKLETON, R. P. & HARVEY, P. H. (2006). Detecting non-brownian trait evolution in adaptive radiations. *Plos Biology* **4**, e373.
- FRETWELL, S. D. & LUCAS, H. L. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16–36.
- FRY, J. D., DONLON, K. & SAWEIKIS, M. (2008). A worldwide polymorphism in aldehyde dehydrogenase in *Drosophila melanogaster*. Evidence for selection mediated by dietary ethanol. *Evolution* **62**, 66–75.
- FULLER, R. M., DEVEREUX, B. J., GILLINGS, S., AMABLE, G. S. & HILL, R. A. (2005). Indices of bird-habitat preference from field surveys of birds and remote sensing of land cover: a study of south-eastern England with wider implications for conservation and biodiversity assessment. *Global Ecology and Biogeography* **14**, 223–239.
- FUSSMAN, G. F., LOREAU, M. & ABRAMS, P. A. (2007). Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology* **21**, 465–477.
- GAVRILETS, S. & LOSOS, J. B. (2009). Adaptive radiation: contrasting theory with data. *Science* **323**, 732–737.
- GAVRILETS, S. & VOSE, A. (2005). Dynamic patterns of adaptive radiation. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 18040–18045.
- GIANOULIS, T. A., RAES, J., PATEL, P. V., BJORNSSON, R., KORBEL, J. O., LETUNIC, I., YAMADA, T., PACCANARO, A., JENSEN, L. J., SNYDER, M., BORK, P., GERSTEIN, M. B. (2009). Quantifying environmental adaptation of metabolic pathways in metagenomics. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 1374–1379.
- GLOR, R. E. (2010). Phylogenetic insights on adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* **41**, 251–270.
- GOLDBERG, E. E., KOHN, J. R., LANDE, R., ROBERTSON, K. A., SMITH, S. A. & IGIC, B. (2010). Species selection maintains self-incompatibility. *Science* **330**, 493–495.
- GOLDBERG, E. E., LANCASTER, L. T. & REE, R. H. (2011). Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Systematic Biology* **60**, 451–465.
- GOLDBERG, E. E., ROY, K., LANDE, R. & JABLONSKI, D. (2005). Diversity, endemism, and age distributions in macroevolutionary sources and sinks. *American Naturalist* **165**, 623–633.
- GONZÁLEZ, J., KARASOV, T. L., MESSER, P. W. & PETROV, D. A. (2010). Genome-wide patterns of adaptation to temperate environments associated with transposable elements in *Drosophila*. *PLoS Genetics* **6**, e1000905.
- GRACE, J. B., HARRISON, S. & DAMSGHEN, E. I. (2011). Local richness along gradients in the Siskiyou herb flora: R. H. Whittaker revisited. *Ecology* **92**, 108–120.
- GRACEY, A. Y., FRASER, E. J., LI, W., FANG, Y., TAYLOR, R. R., ROGERS, J., BRASS, A. & COSSINS, A. R. (2004). Coping with cold: an integrative, multi-tissue analysis of the transcriptome of a poikilothermic vertebrate. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 16970–16975.
- GRANT, P. R. & GRANT, B. R. (1997). Mating patterns of Darwin's finch hybrids determined by song and morphology. *Biological Journal of the Linnean Society* **60**, 317–343.
- GREENE, C. M. (2003). Habitat selection reduces extinction of populations subject to Allee effects. *Theoretical Population Biology* **64**, 1–10.
- GREENE, C. M. & STAMPS, J. A. (2001). Habitat selection at low population densities. *Ecology* **82**, 2091–2100.
- GRIME, J. P., THOMPSON, K., HUNT, R., HODGSON, J. G., CORNELISSEN, J. C. H., RORISON, H. I., HENDRY, G. A. F., ASHENDEN, T. W., ASKEW, A. P., BAND, S. R., BOOTH, R. E., BOSSARD, C. C., CAMPBELL, B. D., COOPER, J. E. L., DAVISON, A. W., GUPTA, P. L., HALL, W., HAND, D. W., HANNAH, M. A., HILLIER, S. H., HODKINSON, D. J., JALILI, A., LIU, Z., MACKEY, J. M. L., MATTHEWS, N., MOWFORTH, M. A., NEAL, A. M., READER, R. J., REILING, K., ROSS-FRASER, W., SPENCER, R. E., SUTTON, F., TASKER, D. E., THORPE, P. C. & WHITEHOUSE, J. (1997). Integrated screening validates primary axes of specialization in plants. *Oikos* **79**, 259–281.
- HAAG, C. R., SAASTAMOINEN, M., MARDEN, J. H. & HANSKI, I. (2005). A candidate locus for variation in dispersal rate in a butterfly metapopulation. *Proceedings of the Royal Society of London Series B—Biological Sciences* **272**, 2449–2456.
- H-ACEVEDO, D. & CURRIE, D. J. (2003). Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. *Global Ecology and Biogeography* **12**, 461–473.
- HADDAD, N. M. & BAUM, K. A. (1999). An experimental test of corridor effects on butterfly densities. *Ecological Applications* **9**, 623–633.
- HAIRSTON, N. G., ELLNER, S. P., GEBER, M. A., YOSHIDA, T. & FOX, J. A. (2005). Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* **8**, 1114–1127.
- HANSKI, I. & MONONEN, T. (2011). Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. *Ecology Letters* **14**, 1025–1034.
- HANSKI, I. & SACCHERI, I. (2006). Molecular-level variation affects population growth in a butterfly metapopulation. *PLoS Biology* **4**, 719–726.
- HANSKI, I. & WOJWOD, I. P. (1993). Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology* **62**, 656–668.
- HARRIS, R. J. & REED, J. M. (2002). Behavioural barriers to non-migratory movements of birds. *Annales Zoologici Fennici* **39**, 275–290.
- HAWKINS, B. A. (2010). Multiregional comparison of the ecological and phylogenetic structure of butterfly species richness gradients. *Journal of Biogeography* **37**, 647–656.

- HAWKINS, B. A., DINIZ-FILHO, J. A., JARAMILLO, C. A. & SOELLER, S. A. (2007). Climate, niche conservatism and the global bird diversity gradient. *American Naturalist* **170**, S16–S27.
- HAWKINS, B. A., FIELD, R., CORNELL, H. V., CURRIE, D. J., GUÉGAN, J. F., KAUFMAN, D. M., KERR, J. T., MITTELBACH, G. G., OBERDORFF, T., O'BRIEN, E. M., PORTER, E. E. & TURNER, J. R. G. (2003a). Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**, 3105–3117.
- HAWKINS, B. A., PORTER, E. E. & DINIZ-FILHO, J. A. F. (2003b). Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology* **84**, 1608–1623.
- HEARD, S. B. & COX, G. H. (2007). The shapes of phylogenetic trees of clades, faunas, and local assemblages: exploring spatial pattern in differential diversification. *American Naturalist* **169**, E108–E118.
- HEARD, S. B. & HAUSER, D. L. (1995). Key evolutionary innovations and their ecological mechanisms. *Historical Biology* **10**, 151–173.
- HEILBUTH, J. C. (2000). Lower species richness in dioecious clades. *American Naturalist* **156**, 221–241.
- HEINZ, S. K., MAZZUCCO, R., DIECKMANN, U. (2009). Speciation and the evolution of dispersal along environmental gradients. *Evolutionary Ecology* **23**, 53–70.
- HELM, B., PIERSMA, T. & VAN DER JEUGD, H. (2006). Sociable schedules: interplay between avian seasonal and social behaviour. *Animal Behaviour* **72**, 245–262.
- HENDRY, A. P., NOSIL, P. & RIESEBERG, L. H. (2007). The speed of ecological speciation. *Functional Ecology* **21**, 455–464.
- HEWITT, G. M. (2001). Speciation, hybrid zones and phylogeography- or seeing genes in space. *Molecular Ecology* **10**, 537–549.
- HILLEBRAND, H. (2004). On the generality of the latitudinal diversity gradient. *American Naturalist* **163**, 192–211.
- HODGES, S. A. & DERIEG, N. J. (2009). Adaptive radiations: from field to genomic studies. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 9947–9954.
- HOEKSTRA, H. E., HIRSCHMANN, R. J., BUNDEY, R. A., INSEL, P. A. & CROSSLAND, J. P. (2006). A single amino acid mutation contributes to adaptive beach mouse color pattern. *Science* **313**, 101–104.
- HOFFMANN, A. A. (2010). Physiological climatic limits in *Drosophila*: patterns and implications. *Journal of Experimental Biology* **213**, 870–880.
- HOFFMANN, A. A., SHIRRIFFS, J. & SCOTT, M. (2005). Relative importance of plastic vs genetic factors in adaptive differentiation: geographical variation for stress resistance in *Drosophila melanogaster* from Eastern Australia. *Functional Ecology* **19**, 222–227.
- HOHENLOHE, P. A., BASSHAM, S., ETTER, P. D., STIFFLER, N., JOHNSON, E. A. & CRESKO, W. A. (2010). Population genomics of parallel adaptation in threespine stickleback using sequenced RAD tags. *PLoS Genetics* **6**, e1000862.
- HOLYOAK, M., CASAGRANDI, R., NATHAN, R., REVILLA, E. & SPIEGEL, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 19060–19065.
- HONKANEN, M., ROBERGE, J. M., RAJASÄRKÄ, A. & MÖNKKÖNEN, M. (2010). Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. *Global Ecology and Biogeography* **19**, 61–71.
- HOULE, D., GOVINDARAJU, D. R. & OMHOLT, S. (2010). Phenomics: the next challenge. *Nature Reviews Genetics* **11**, 855–866.
- HUBBELL, S. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, USA.
- HUEY, R. B., HERTZ, P. E. & SINERVO, B. (2003). Behavioural drive versus behavioural inertia in Evolution: a null model approach. *American Naturalist* **161**, 357–366.
- HUGHES, C. & EASTWOOD, R. (2006). Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 10334–10339.
- HUGUENY, B., CORNELL, H. V. & HARRISON, S. (2007). Metacommunity models predict the local-regional species richness relationship in a natural system. *Ecology* **88**, 1696–1706.
- HURLBERT, A. H. (2004). Species-energy relationships and habitat complexity in bird communities. *Ecology Letters* **7**, 714–720.
- HURLBERT, A. H. & HASKELL, J. P. (2003). The effect of energy and seasonality on avian species richness and community composition. *American Naturalist* **161**, 83–97.
- HUTCHINSON, G. E. (1959). Homage to Santa Rosalia or Why are there so many kinds of animals? *American Naturalist* **93**, 145–159.
- IGCI, B., LANDE, R. & KOHN, J. R. (2008). Loss of self-incompatibility and its evolutionary consequences. *International Journal of Plant Sciences* **169**, 93–104.
- IRWIN, D. E. (2000). Song variation in avian ring species. *Evolution* **54**, 998–1010.
- IRWIN, D. E., BENSCH, S., IRWIN, J. H. & PRICE, T. D. (2005). Speciation by distance in a ring species. *Science* **307**, 414–416.
- IRWIN, D. E., BENSCH, S. & PRICE, T. D. (2001a). Speciation in a ring. *Nature* **409**, 333–337.
- IRWIN, D. E. & IRWIN, J. H. (2005). Siberian migratory divides: the role of seasonal migration in speciation. In: *Birds of the two worlds: the Ecology and Evolution of Migration*. (eds R. GREENBERG and P. P. MARRA) pp. 27–40. Johns Hopkins University Press, Baltimore.
- IRWIN, D. E., IRWIN, J. H. & PRICE, T. D. (2001b). Ring species as bridges between microevolution and speciation. *Genetica* **112**, 223–243.
- IRWIN, D. E., THIMGAN, M. P. & IRWIN, J. H. (2008). Call divergence is correlated with geographic and genetic distance in greenish warblers (*Phylloscopus trochiloides*): a strong role for stochasticity in signal evolution? *Journal of Evolutionary Biology* **21**, 435–448.
- JABLONSKI, D., ROY, K. & VALENTINE, J. W. (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* **314**, 102–106.
- JANZ, N. & NYLIN, S. (2008). The oscillation hypothesis of host plant-range and speciation. In: *Specialization, Speciation, and Radiation: the Evolutionary Biology of Herbivorous Insects* (ed. K. J. TILMON) pp. 203–215. University of California Press, Berkeley, USA.
- JENSEN, J. D., WONG, A. & AQUADRO, C. F. (2007). Approaches for identifying targets of positive selection. *Trends in Genetics* **23**, 568–577.
- JESCHKE, J. M. & KOKKO, H. (2009). The roles of body size and phylogeny in fast and slow life histories. *Evolutionary Ecology* **23**, 867–878.
- JETZ, W. & RAHBEK, C. (2002). Geographic range size and determinants of avian species richness. *Science* **297**, 1548–1551.
- JETZ, W. & RUBENSTEIN, D. R. (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology* **21**, 72–78.
- JETZ, W., SEKERCIOGLU, C. H. & BÖHNING-GAESE, K. (2008). The worldwide variation in avian clutch size across species and space. *PLoS Biology* **6**, e303.
- JOHANSSON, U. S., ALSTRÖM, P., OLSSON, U., ERICSON, P. G. P., SUNDBERG, P. & PRICE, T. D. (2007). Build up of the Himalayan avifauna through immigration: a biogeographical analysis of the *Phylloscopus* and *Seiurus* warblers. *Evolution* **61**, 324–333.
- JOHNSON, M. D. (2007). Measuring habitat quality: a review. *Condor* **109**, 489–504.
- JOHNSON, M. D., SHERRY, T. W., STRONG, A. M. & MEDORI, A. (2005). Migrants in neotropical bird communities: an assessment of the breeding currency hypothesis. *Journal of Animal Ecology* **74**, 333–341.
- JOHNSON, M. T. J. & STINCHCOMBE, J. R. (2007). An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology and Evolution* **22**, 250–256.
- JOHNSON, N. K. & CICERO, C. (2004). New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. *Evolution* **58**, 1122–1130.
- KADMON, R. & ALLOUCHE, O. (2007). Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *American Naturalist* **170**, 443–454.
- KARL, I., SCHMITT, T. & FISCHER, K. (2009). Genetic differentiation between alpine and lowland populations of a butterfly is related to PGI enzyme genotype. *Ecography* **32**, 488–496.
- KEARNEY, M. & PORTER, W. (2009). Mechanistic niche modeling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**, 334–350.
- KELLERMANN, V., VAN HEERWAARDEN, B., SGRÖ, C. M. & HOFFMANN, A. A. (2009). Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science* **325**, 1244–1246.
- KISSLING, W. D., BÖHNING-GAESE, K. & JETZ, W. (2009). The global distribution of frugivory in birds. *Global Ecology and Biogeography* **18**, 150–162.
- KISSLING, W. D., SEKERCIOGLU, C. H. & JETZ, W. (2011). Bird dietary guild richness across latitudes, environments and biogeographic regions. *Global Ecology & Biogeography*. On line early view.
- KLEMM, I. & HANSKI, I. (2009). Heritability of and strong single gene (Pgi) effects on life-history traits in the Glanville fritillary butterfly. *Journal of Evolutionary Biology* **22**, 1944–1953.
- KOH, L. P., SODHI, N. S. & BROOK, B. W. (2004). Ecological correlates of extinction processes in tropical butterflies. *Conservation Biology* **18**, 1571–1578.
- KOLACZKOWSKI, B., KERN, A. D., HOLLOWAY, A. K. & BEGUN, D. J. (2011). Genomic differentiation between temperate and tropical Australian populations of *Drosophila melanogaster*. *Genetics* **187**, 245–60.
- KONDOH, M. (2003). Foraging adaptation and the relationship between food-web complexity and stability. *Science* **299**, 1388–1391.
- KOTIAHO, J. S., KAITALA, V., KOMONEN, A. & PÄIVINEN, J. (2005). Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 1963–1967.
- KOZAK, K. H. & WIENS, J. J. (2011). Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters* **13**, 1378–1389.
- KOZAK, K. H. & WIENS, J. J. (2010). Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *The American Naturalist* **176**, 40–54.
- KRAFT, N. J. B., COMITA, L. S., CHASE, J. M., SANDERS, N. J., SWENSON, N. G., CRIST, T. O., STEGEN, J. C., VELLEND, M., ANDERSON, M. J., CORNELL, H. V., DAVIES, K. F., FREESTONE, A. L., INNOUYE, B. D., HARRISON, S. P. & MYERS, J. A. (2011). Disentangling the drivers of beta-diversity along latitudinal and elevational gradients. *Science* **333**, 1755–1758.
- KRAFT, N. J. B., CORNWELL, W. K., WEBB, C. O. & ACKERLY, D. D. (2007). Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist* **170**, 271–283.
- KRAUSS, J., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. (2003). Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. *Oecologia* **137**, 591–602.



- KRONFORST, M. R., YOUNG, L. G., KAPAN, D. D., MCNEELY, C., O'NEILL, R. J. & GILBERT, L. E. (2006). Linkage of butterfly mate preference and wing color preference cue at the genomic location of wingless. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 6575–6580.
- KUUSAAARI, M., NIEMINEN, M. & HANSKI, I. (1996). An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology* **65**, 791–801.
- KUUSAAARI, M., SACCHERI, I., CAMARA, M. & HANSKI, I. (1998). Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos* **82**, 384–392.
- KYRIACOU, C. P., PEIXOTO, A. A., SANDRELLI, F., COSTA, R. & TAUBER, E. (2008). Clines in clock genes. *Trends in Genetics* **24**, 124–132.
- LAURO, F. M., MCDUGALD, D., THOMAS, T., WILLIAMS, T. J., EGAN, S., RICE, S., DEMAERE, M. Z., TING, L., ERTAN, H., JOHNSON, J., FERREIRA, S., LAPIDUS, A., ANDERSON, I., KYRPIDES, N., MUNK, A. C., DETTER, C., HAN, C. S., BROWN, M. V., ROBB, F. T., KJELLEBERG, S. & CAVICCHIOLI, R. (2009). The genomic basis of marine bacteria. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 15527–15533.
- LEFEBVRE, L., WHITTLE, P., LASCARIS, E. & FINKELSTEIN, A. (1997). Feeding innovations and forebrain size in birds. *Animal Behaviour* **53**, 549–560.
- LENNON, J. J., BEALE, C. M., REID, C. L., KENT, M. & PAKEMAN, R. J. (2011). Are richness patterns of common and rare species equally well explained by environmental variables? *Ecography* **34**, 529–539.
- LENNON, J. J., GREENWOOD, J. J. D. & TURNER, J. R. G. (2000). Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. *Journal of Animal Ecology* **69**, 581–598.
- LEVEY, D. J. (1988). Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* **58**, 251–269.
- LEVEY, D. J. & STILES, F. G. (1992). Evolutionary precursors of long-distance migration: resource availability and movement patterns in neotropical landbirds. *American Naturalist* **140**, 447–476.
- LEVINTON, J. S. (1979). A theory of diversity equilibrium and morphological evolution. *Science* **204**, 335–336.
- LEVRIJA-TREJOS, E., PÉREZ-GARCÍA, E. A., MEAVE, J. A., BONGERS, F. & POORTER, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* **91**, 386–398.
- LIEDVOGEL, M., SZULKIN, M., KNOWLES, S. C. L., WORD, M. J. & SHELDON, B. C. (2009). Phenotypic correlates of Clock gene variation in a wild blue tit population: evidence for a role in seasonal timing of reproduction. *Molecular Ecology* **18**, 2444–2456.
- LITCHMAN, E. & KLAUSMEIER, C. A. (2008). Trait-based community ecology of phytoplankton. *Annual Review of Ecology, Evolution and Systematics* **39**, 615–639.
- LOISELLE, B. A. (1988). Bird abundance and seasonality in a Costa Rican Lowland forest canopy. *Condor* **90**, 761–772.
- LOISELLE, B. A. & BLAKE, J. G. (1991). Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* **72**, 180–193.
- LOVETTE, I. J. (2005). Glacial cycles and the tempo of avian speciation. *Trends in Ecology and Evolution* **20**, 57–59.
- LOVETTE, I. & HOCHACHKA, W. (2006). Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology* **87**, S14–S28.
- MACARTHUR, R., RECHER, H. & CODY, M. (1966). On the relation between habitat selection and species diversity. *American Naturalist* **100**, 319–332.
- MACARTHUR, R. H. & WILSON, E. O. (1963). An equilibrium theory of insular biogeography. *Evolution* **17**, 373–387.
- MACEL, M., VAN DAM, N. M. & KEURENTJES, J. J. B. (2010). Metabolomics: the chemistry between ecology and genetics. *Molecular Ecology Resources* **10**, 583–593.
- MALLARINO, R., HERREL, A., KUO, W. P., GRANT, B. R., GRANT, P. R. & ABZHANOV, A. (2011). Two developmental modules establish 3D beak-shape variation in Darwin's finches. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 4057–4062.
- MASAKI, S. (1999). Seasonal adaptations of insects as revealed by latitudinal diapause clines. *Entomological Science* **2**, 539–549.
- MCBRIDE, C. S. & ARGUELLO, J. R. (2007). Five *Drosophila* genomes reveal nonneutral evolution and the signature of host specialization in the chemoreceptor superfamily. *Genetics* **177**, 1395–1416.
- MCBRIDE, C. S. & SINGER, M. C. (2010). Field studies reveal strong postmating isolation between ecologically divergent butterfly populations. *PLoS Biology* **8**, e1000529.
- McKINNON, L., SMITH, P. A., NOL, E., MARTIN, J. L., DOYLE, F. I., ABRAHAM, K. F., GILCHRIST, H. G., MORRISON, R. I. & BÉTY, J. (2010). Lower predation risk for migratory birds at high latitudes. *Science* **327**, 326–327.
- MCPEEK, M. A. (1996). Linking local species interactions to rates of speciation in communities. *Ecology* **77**, 1355–1366.
- MEEHAN, T. D., JETZ, W. & BROWN, J. H. (2004). Energetic determinants of abundance in winter landbird communities. *Ecology Letters* **7**, 532–537.
- MELBOURNE, B. A. & HASTINGS, A. (2008). Extinction risk depends strongly on factors contributing to stochasticity. *Nature* **454**, 100–104.
- MENKEN, S. B. J., BOOMSMA, J. J. & VAN NIEUKERKEN, E. J. (2009). Large-scale evolutionary patterns of host plant associations in the Lepidoptera. *Evolution* **64**, 1098–1119.
- METTKE-HOFMANN, C. & GWINNER, E. (2004). Differential assessment of environmental information on a migratory and a nonmigratory passerine. *Animal Behaviour* **68**, 1079–1086.
- MICHEL, A. P., SIM, S., POWELL, T., NOSIL, P. & FEDER, J. L. (2010). Widespread genomic divergence during sympatric speciation. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 9724–9729.
- MITTELBACH, G. G., SCHEMSKE, D. W., CORNELL, H. V., ALLEN, A. P., BROWN, J. M., BUSH, M. B., HARRISON, S. P., HURLBERT, A. H., KNOWLTON, N., LESSIOS, H. A., MCCAIN, C. M., MCCUNE, A. R., MCDADE, L. A., MCPREEK, M. A., NEAR, T. J., PRICE, T. D., RICKLEFS, R. E., ROY, K., SAX, D. F., SCHLUTER, D., SOBEL, J. M. & TURELLI, M. (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* **10**, 315–331.
- MİYASATO, L. E. & BAKER, M. C. (1999). Black-capped chickadee call dialects along a continuous habitat corridor. *Animal Behaviour* **57**, 1311–1318.
- MOCZEK, A. P., SULTAN, S., FOSTER, S., LEDON-RETTIG, C., DWORNIK, I., NIJHOUT, H. F., ABOUHEIF, E. & PFENNIG, D. (2011). The role of developmental plasticity in evolutionary innovation. *Proceedings of the Royal Society of London, Series B* **278**, 2705–2713.
- MOLES, A. T., WARTON, D. I., STEVENS, R. D. & WESTOBY, M. (2004). Does a latitudinal gradient in seedling survival favour larger seeds in the tropics? *Ecology Letters* **7**, 911–914.
- MOLES, A. T. & WESTOBY, M. (2003). Latitude, seed predation and seed mass. *Journal of Biogeography* **30**, 105–128.
- MØLLER, A. P. & CUERVO, J. J. (1998). Speciation and feather ornamentation in birds. *Evolution* **52**, 859–869.
- MÖNKKÖNEN, M., FORSMAN, J. T. & BOKRNA, F. (2006). Energy availability, abundance, energy-use and species richness in forest bird communities: a test of the species-energy theory. *Global Ecology and Biogeography* **15**, 290–302.
- MÖNKKÖNEN, M., HELLE, P. & SOPPELA, K. (1990). Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? *Oecologia* **85**, 218–225.
- MONTESINOS-NAVARRO, A., WIG, J., PICO, X. & TONSOR, S. J. (2011). *Arabidopsis thaliana* populations show clinal variation in a climatic gradient associated with altitude. *New Phytologist* **189**, 282–294.
- MOORE, B. R. & DONOGHUE, M. J. (2007). Correlates of diversification in the plant clade Dipsacales: geographic movement and evolutionary innovations. *American Naturalist* **170**, S28–S55.
- MOORE, R. P., ROBINSON, W. D., LOVETTE, I. J., ROBINSON, T. R. (2008). Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters* **11**, 960–968.
- MORRIS, D. W. (2003). Toward an ecological synthesis: a case for habitat selection. *Oecologia* **136**, 1–13.
- MOYA-LARAÑO, J. (2010). Can temperature and water availability contribute to the maintenance of latitudinal diversity by increasing the rate of biotic interactions? *The Open Ecology Journal* **3**, 1–13.
- MOYLE, R. G., FILARDI, C. E., SMITH, C. E. & DIAMOND, J. (2009). Explosive Pleistocene diversification and hemispheric expansion of a “great speciator”. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 1863–1868.
- NAISH, K. A. & HARD, J. J. (2008). Bridging the gap between the genotype and the phenotype: linking genetic variation, selection and adaptation in fishes. *Fish and Fisheries* **9**, 396–422.
- NATHAN, R., GETZ, W. M., REVILLA, E., HOLYOAK, M., KADMON, R., SALTZE, D. & SMOUSE, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 19052–19059.
- NÈVE, G. (2009). Population genetics of butterflies. In: *Ecology of butterflies in Europe* (eds J. SETTELE, T. SHREEVE, M. KONVICKA and H. VAN DYCK) pp. 107–129. Cambridge University Press, Cambridge, UK.
- NIITEPÖLD, K., SMITH, A. D., OSBORNE, J. L., REYNOLDS, D. R., CARRECK, N. L., MARTIN, A. P., MARDEN, J. H., OVASKAINEN, O. & HANSKI, I. (2009). Flight metabolic rate and Pgi genotype influence butterfly dispersal rate in the field. *Ecology* **90**, 2223–2232.
- NOSIL, P., FUNK, D. J. & ORTIZ-BARRIENTOS, D. (2009). Divergent selection and heterogeneous genomic divergence. *Molecular Ecology* **18**, 375–402.
- NOSIL, P. & SCHLUTER, D. (2011). The genes underlying the process of speciation. *Trends in Ecology and Evolution* **26**, 160–167.
- NOVOTNY, V., MILLER, S. E., HULCR, J., DREW, R. A. I., BASSETT, Y., JANDA, M., SETLIFF, G. P., DARROW, K., STEWART, A. J. A., AUGA, J., ISUA, B., MOLEM, K., MANUMBOR, M., TAMTIAT, E., MOGIA, M., & WEIBLEN, G. D. (2007). Low beta diversity of herbivorous insects in tropical forests. *Nature* **448**, 692–697.
- OLESEN, J. & JORDANO, P. (2002). Geographic patterns in plant-pollinator mutualistic networks. *Ecology* **83**, 2416–2424.
- OLIVER, T., ROY, D. B., HILL, J. K., BRERETON, T. & THOMAS, C. D. (2010). Heterogeneous landscapes promote population stability. *Ecology Letters* **13**, 473–484.
- ORR, H. A. (2009). Fitness and its role on evolutionary genetics. *Nature Reviews Genetics* **10**, 531–539.

- ORROCK, J. L. & FLETCHER, R. J. (2005). Changes in community size affect the outcome of competition. *American Naturalist* **166**, 107–111.
- OVASKAINEN, O., SMITH, A. D., OSBORNE, J. L., REYNOLDS, D. R., CARRECK, N. L., MARTIN, A. P., NIITEPÖLD, K. & HANSKI, I. (2008). Tracking butterfly movements with harmonic radar reveals an effect of population age on movement distance. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 19090–19095.
- PAABY, A. B., BLACKET, M. J., HOFFMANN, A. A. & SCHMIDT, P. S. (2010). Identification of a candidate adaptive polymorphism for *Drosophila* life history by parallel independent clines on two continents. *Molecular Ecology* **19**, 760–774.
- PALSSON, B. (2009). Metabolic systems biology. *FEBS Letters* **583**, 3900–3904.
- PARADIS, E. (2005). Statistical analysis of diversification with species traits. *Evolution* **59**, 1–12.
- PARADIS, E., BAILLIE, S. R., SUTHERLAND, W. J. & GREGORY, R. D. (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* **67**, 518–536.
- PARCHMAN, T. L. & BENKMAN, C. W. (2002). Diversifying coevolution between crossbills and black spruce on Newfoundland. *Evolution* **56**, 479–501.
- PAJEJO, D., WHITE, J., CLOBERT, J., DREISS, A. & DANCHIN, E. (2007). Blue tits use fledging quantity and quality as public information in breeding site choice. *Ecology* **88**, 2373–2382.
- PÄRTEL, M. (2002). Local plant diversity patterns and evolutionary history at the regional scale. *Ecology* **83**, 2361–2366.
- PÄRTEL, M., LAANISTO, L. & ZOBEL, M. (2007). Contrasting plant productivity-diversity relationships in temperate and tropical regions: the role of evolutionary history. *Ecology* **88**, 1091–1097.
- PATTEN, M. A., ROTENBERRY, J. T. & ZUK, M. (2004). Habitat selection, acoustic adaptation and the evolution of reproductive isolation. *Evolution* **58**, 2144–2155.
- PAUTASSO, M. & GASTON, K. J. (2005). Resources and global avian assemblage structure in forests. *Ecology Letters* **8**, 282–289.
- PAVLIDIS, P., HUTTER, S. & STEPHAN, W. (2008). A population genomic approach to map recent positive selection in model species. *Molecular Ecology* **17**, 3585–3598.
- PETERS, V. E., MORDECAI, R., RONALD CARROLL, C., COOPER, R. J. & GREENBERG, R. (2010). Bird community response to fruit energy. *Journal of Animal Ecology* **79**, 824–835.
- PFENNIG, D. W., WUND, M. A., SNELL-ROOD, E. C., CRUICKSHANK, T., SCHLICHTING, C. D. & MOCZEK, A. P. (2010). Phenotypic plasticity's impacts on diversification and speciation. *Trends in Ecology and Evolution* **25**, 459–467.
- PHILLIMORE, A. B., FRECKLETON, R. P., ORME, C. D., OWENS, I. P. (2006). Ecology predicts large-scale patterns of phylogenetic diversification in birds. *American Naturalist* **168**, 220–229.
- PHILLIMORE, A. B., ORME, C. D. L., DAVIES, R. G., HADFIELD, J. D., REED, W. J., GASTON, K. J., FRECKLETON, R. P. & OWENS, I. P. F. (2007). Biogeographical basis of recent phenotypic divergence among birds: a global study of subspecies richness. *Evolution* **61**, 942–957.
- PIGLIUCCI, M. (2010). Genotype-phenotype mapping and the end of the “genes as blueprint” metaphor. *Philosophical Transactions of the Royal Society of London Series B* **365**, 557–566.
- PIGOT, A. L., PHILLIMORE, A. B., OWENS, I. P. & ORME, C. D. (2010). The shape and temporal dynamics of phylogenetic trees arising from geographic speciation. *Systematic Biology* **59**, 660–673.
- PIMENTEL, D. (1961). Animal population regulation by the genetic feed-back mechanism. *American Naturalist* **97**, 141–167.
- PODOS, J. (2001). Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* **409**, 185–188.
- POORTER, L., WRIGHT, S. J., PAZ, H., ACKERLY, D. D., CONDIT, R., IBARRA-MANRIQUEZ, G., HARMS, K. E., LICONA, J. C., MARTINEZ-RAMOS, M., MAZER, S. J., MÜLLER-LANDAU, H. C., PEÑA-CLAROS, M., WEBB, C. O. & WRIGHT, I. (2008). Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology* **89**, 1908–1920.
- POULIN, B. & LEFEBVRE, G. (1996). Dietary relationships of migrant and resident birds from a humid forest in central Panama. *Auk* **113**, 277–287.
- PRESGRAVES, D. C. (2010). The molecular evolutionary basis of species formation. *Nature Reviews Genetics* **11**, 175–180.
- PRICE, T. D. (1998). Sexual selection and natural selection in bird speciation. *Philosophical Transactions of the Royal Society of London B-Biological Sciences* **353**, 251–260.
- PRICE, T. D. (2008). *Speciation in birds*. Roberts and Company, Greenwood Village, Colorado, USA.
- PRICE, T. D., QVARNSTRÖM, A. & IRWIN, D. E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal B-Biological Sciences* **270**, 1433–1440.
- PRUD'HOMME, B., GOMPEL, N. & CARROLL, S. B. (2007). Emerging principles of regulatory evolution. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 8605–8612.
- PYBUS, O. G. & HARVEY, P. H. (2000). Testing macro-evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**, 2267–2272.
- RABOSKY, D. L. (2009). Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters* **12**, 735–743.
- RABOSKY, D. L. (2010). Extinction rates should not be estimated from molecular phylogenies. *Evolution* **6**, 1816–1824.
- RAES, J., LETUNIC, I., YAMADA, T., JENSEN, L. J., BORK, P. (2011). Toward molecular trait-based ecology through integration of biogeochemical, geographical and metagenomic data. *Molecular Systems Biology* **7**, 473.
- RANGEL, T. F. L. V. B. & DINIZ-FILHO, J. A. F. (2005). Neutral community dynamics, the middomain effect and spatial patterns in species richness. *Ecology Letters* **8**, 783–790.
- RANGEL, T. F. L. V. B., DINIZ-FILHO, J. A. F. & COLWELL, R. K. (2007). Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. *American Naturalist* **170**, 602–616.
- RANK, N. E. & DAHLOFF, E. P. (2002). Allele frequency shifts in response to climate change and physiological consequences of allozyme variation in a montane insect. *Evolution* **56**, 2278–2289.
- RASMANN, S. & AGRAWAL, A. A. (2011). Latitudinal patterns in plant defense: evolution of cardenolides, their toxicity and induction following herbivory. *Ecology Letters* **14**, 476–483.
- REE, R. H. (2005). Detecting the historical signature of key innovations using stochastic models of character evolution and cladogenesis. *Evolution* **59**, 257–265.
- REE, R. H., MOORE, B. R., WEBB, C. O. & DONOGHUE, M. J. (2005). A likelihood method for inferring the evolution of geographic range on phylogenetic trees. *Evolution* **59**, 2299–2311.
- REED, J. M. (1999). The role of behaviour in recent avian extinctions and endangerments. *Conservation Biology* **13**, 232–241.
- REED, J. M. & LEVINE, S. H. (2005). A model for behavioural regulation of metapopulation dynamics. *Ecological Modelling* **183**, 411–423.
- REICH, P. B. & OLEKSYN, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 11001–11006.
- REICH, P. B., WALTERS, M. B. & ELLSWORTH, D. S. (1997). From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America* **94**, 13730–13734.
- REMSEN, J. V. (2003). The Coerebidae: a polyphyletic taxon that dramatizes historical over-emphasis on bill shape as a taxonomic character. *Journal of Avian Biology* **34**, 321–323.
- REVILLA, E. & WIEGAND, T. (2008). Individual movement behaviour, matrix heterogeneity and the dynamics of spatially structured populations. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 19120–19125.
- RICE, A. M., RUDH, A., ELLEGREN, H. & QVARNSTRÖM, A. (2011). A guide to the genomics of ecological speciation in natural animal populations. *Ecology Letters* **14**, 9–18.
- RICHMAN, A. D. (1996). Ecological diversification and community structure of old world leaf warblers (genus *Phylloscopus*): a phylogenetic perspective. *Evolution* **50**, 2461–2470.
- RICKLEFS, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters* **7**, 1–15.
- RICKLEFS, R. E. (2006a). Evolutionary diversification and the origin of the diversity-environment relationship. *Ecology* **87**, S3–S13.
- RICKLEFS, R. E. (2006b). Global variation in the diversification rate of passerine birds. *Ecology* **87**, 2468–2487.
- RICKLEFS, R. E. (2007). History and diversity: explorations at the intersection of ecology and evolution. *American Naturalist* **170**, S56–S70.
- RICKLEFS, R. E. & BERMINGHAM, E. (2001). Nonequilibrium diversity dynamics of the Lesser Antillean avifauna. *Science* **294**, 1522–1524.
- RICKLEFS, R. E. & BERMINGHAM, E. (2004). Application of Johnson et al's speciation threshold model to apparent colonization times of island biotas. *Evolution* **58**, 1664–1673.
- RICKLEFS, R. E. & RENNER, S. S. (1994). Species richness within families of flowering plants. *Evolution* **48**, 1619–1636.
- RIES, L. & DEBINSKI, D. M. (2001). Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. *Journal of Animal Ecology* **70**, 840–852.
- RIESEBERG, L. H. & BLACKMAN, B. K. (2010). Speciation genes in plants. *Annals of Botany* **106**, 439–455.
- ROHDE, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527.
- ROSENZWEIG, M. L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, New York, USA.
- ROSINDELL, J. & PHILLIMORE, A. B. (2011). A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters* **14**, 552–560.
- ROY, K. & GOLDBERG, E. E. (2007). Origination, extinction, and dispersal: integrative models for understanding present-day diversity gradients. *American Naturalist* **170**, S71–S85.
- RUEFFLER, C., VAN DOOREN, T. J. & METZ, J. A. (2007). The interplay between behaviour and morphology in the evolutionary dynamics of resource specialization. *American Naturalist* **168**, E34–E52.



- SÆTHER, B.-E., ENGEN, S. & LANDE, R. (1999). Finite metapopulation models with density-dependent migration and stochastic local dynamics. *Proceedings of the Royal Society of London Series B- Biological Sciences* **266**, 113–118.
- SÆTHER, B.-E., ENGEN, S., MØLLER, A. P., MATTHYSEN, E., ADRIANSEN, F., FIEDLER, W., LEIVITS, A., LAMBRECHTS, M. M., VISSER, M. E., ANKER-NILSSE, T., BOTH, C., DHOND, A. A., MCCLEERY, R. H., McMEEKING, J., POTTI, J., RØSTAD, O. & THOMSON, D. (2003). Climate variation and regional gradients in population dynamics of two hole-nesting passerines. *Proceedings of the Royal Society of London Series B- Biological Sciences* **270**, 2397–2404.
- SÆTHER, B.-E., GRØTAN, V., ENGEN, S., NOBLE, D. G. & FRECKLETON, R. P. (2011). Rarity, life history and scaling of the dynamics in time and space of British birds. *Journal of Animal Ecology* **80**, 215–224.
- SÆTHER, B.-E., LILLEGÅRD, M., GRØTAN, V., DREVER, M. C., ENGEN, S., NUDDS, T. D. & PODRUZNY, K. M. (2008). Geographical variation in the population dynamics of North American prairie ducks. *Journal of Animal Ecology* **77**, 869–882.
- SÆTRE, G.-P., BORGE, T., LINDELL, J., MOUM, T., PRIMMER, C. R., SHELDON, B. C., HAAVIE, J., JOHNSEN, A. & ELLEGREN, H. (2001). Speciation, introgressive hybridization and nonlinear rate of molecular evolution in flycatchers. *Molecular Ecology* **10**, 737–749.
- SÆTRE, G.-P. & SÆTHER, S. A. (2010). Ecology and genetics of speciation in *Ficedula* flycatchers. *Molecular Ecology* **19**, 1091–1106.
- SAASTAMOINEN, M. & HANSKI, I. (2008). Genotypic and environmental effects on flight activity and ovoposition in the Glanville fritillary butterfly. *American Naturalist* **171**, 701–712.
- SACCHERI, I., KUUSSAARI, M., KANKARE, M., VIKMAN, P., FORTELIUS, W. & HANSKI, I. (1998). Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**, 491–494.
- SALEWSKI, V. & BRUDERER, B. (2007). The evolution of bird migration. A synthesis. *Naturwissenschaften* **94**, 268–279.
- SARGENT, R. D. (2004). Floral asymmetry affects speciation rates in angiosperms. *Proceedings of the Royal Society of London B* **271**, 603–608.
- SCHNEIDER, S. M. & WILLIG, M. R. (2005). Developing unified theories in Ecology as exemplified with diversity gradients. *American Naturalist* **166**, 458–469.
- SCHEMSKE, D. W., MITTELBAUGH, G. G., CORNELL, H. V., SOBEL, J. M. & ROY, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics* **40**, 245–269.
- SCHLEUNING, M., BLÜTHGEN, N., FLÖRCHINGER, M., BRAUN, J., MARTIN SCHAEFER, H. & BÖHNING-GAESE, K. (2011). Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. *Ecology* **92**, 26–36.
- SCHLUTER, D. (2009). Evidence for ecological speciation and its alternative. *Science* **323**, 737–741.
- SCHMIDT, P. S. & PAABY, A. B. (2008). Reproductive diapause and life-history clines in North American populations of *Drosophila melanogaster*. *Evolution* **62**, 1204–1215.
- SCHMIDT, P. S., SERRAO, E. A., PEARSON, G. A., RIGINOS, C., RAWSON, P. D., HILBISH, T. J., BRAWLEY, S. H., TRUSSELL, G. C., CARRINGTON, E., WETHEY, D. S., GRAHAME, J. W., BONHOMME, F. & RAND, D. M. (2008a). Ecological genetics in the North Atlantic: environmental gradients and adaptation at specific loci. *Ecology* **89**, S91–S107.
- SCHMIDT, P. S., ZHU, C. T., DAS, J., BATAVIA, M., YANG, L. & EANES, W. F. (2008b). An amino acid polymorphism in the couch potato gene forms the basis for climatic adaptation in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 16207–16211.
- SCRIBER, J. M. (1973). Latitudinal gradients in larval feeding specialization of the world Papilionidae (Lepidoptera). *Psyche* **80**, 355–373.
- SEDDON, N. (2005). Ecological adaptation and species recognition drives vocal evolution in Neotropical subsocial birds. *Evolution* **59**, 97–112.
- SEDDON, N., MERRILL, R. M. & TOBIAS, J. A. (2008). Sexually selected traits predict patterns of species richness in a diverse clade of subsocial birds. *American Naturalist* **171**, 620–631.
- SEEHAUSEN, O., TERAI, Y., MAGALHAE, I. S., CARLETON, K. L., MROSSO, H. D. J., MIYAGI, R., VAN DER SLUIJS, I., SCHNEIDER, M. V., MAAN, M. E., TACHIDA, H., IMAI, H. & OKADA, N. (2008). Speciation through sensory drive in cichlid fish. *Nature* **455**, 620–626.
- SHAPIRO, M. D., MARKS, M. E., PEICHEL, C. L., BLACKMAN, B. K., NERENG, K. S., JONSSON, B., SCHLUTER, D. & KINGSLEY, D. M. (2004). Genetic and developmental basis of evolutionary pelvic reduction in threespine sticklebacks. *Nature* **428**, 717–723.
- SHULTZ, S., BRADBURY, R. B., EVANS, K. L., GREGORY, R. D. & BLACKBURN, T. M. (2005). Brain size and resource specialization predict long-term population trends in British birds. *Proceedings of the Royal Society of London Series B- Biological Sciences* **272**, 2305–2311.
- SILVERTOWN, J., DODD, M., GOWING, D., LAWSON, C. & MCCONWAY, K. (2006). Phylogeny and the hierarchical organization of plant diversity. *Ecology* **87**, S39–S49.
- SINGH, N. D., LARRACUENTE, A. M., SACKTON, T. B. & CLARK, A. G. (2009). Comparative genomics on the *Drosophila* phylogenetic tree. *Annual Review of Ecology, Evolution, and Systematics* **40**, 459–480.
- SIRAMI, C., BROTONS, L. & MARTIN, J. L. (2008). Spatial extent of bird responses to landscape changes: colonisation/extinction dynamics at the community-level in two contrasting habitats. *Ecography* **31**, 509–518.
- SLABBEKOORN, H. & SMITH, T. B. (2002a). Bird song, ecology, and speciation. *Philosophical Transactions of the Royal Society of London Series B* **357**, 493–503.
- SLABBEKOORN, H. & SMITH, T. B. (2002b). Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection. *Evolution* **56**, 2144–2155.
- SLATE, J., GRATTEN, J., BERARDI, D., STAPLEY, J., HALE, M. & PEMBERTON, J. M. (2009). Gene mapping in the wild with SNPs: guidelines and future directions. *Genetica* **136**, 97–107.
- SMITH, S. A. & DONOGHUE, M. J. (2008). Rates of molecular evolution are linked to life history in flowering plants. *Science* **322**, 86–89.
- SMITH, S. A., NIETO MONTES DE OCA, A., REEDER, T. W. & WIENS, J. J. (2008). A phylogenetic perspective on latitudinal species richness gradients in middle American treefrogs: why so few species in lowland tropical rain forests? *Evolution* **61**, 1188–1207.
- SMITH, T. B., WAYNE, R. K., GIRMAN, D. J. & BRUFORD, M. W. (1997). A role for ecotones in generating rainforest biodiversity. *Science* **276**, 1855–1857.
- SNELL-ROOD, E. C. & BADIYAEV, A. V. (2008). Ecological gradient of sexual selection: elevation and song elaboration in finches. *Oecologia* **157**, 545–551.
- SNELL-ROOD, E. C., VANDYKEN, J. D., CRUICKSHANK, T. E., WADE, M. J., MOCZEK, A. P. (2010). Toward a population genetic framework of developmental evolution: costs, limits, and consequences of phenotypic plasticity. *Bioessays* **32**, 71–81.
- SOBERÓN, J. (2007). Grinnellian and Eltonian niches and geographic distribution of species. *Ecology Letters* **10**, 1115–1123.
- SOL, D., DUNCAN, R. P., BLACKBURN, T. M., CASSEY, P. & LEFEBVRE, L. (2005a). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 5460–5465.
- SOL, D. & PRICE, T. D. (2008). Brain size and body size diversification in birds. *American Naturalist* **172**, 170–177.
- SOL, D., STIRLING, D. G. & LEFEBVRE, L. (2005b). Behavioural drive or behavioural inhibition in evolution: subspecific diversification in holarctic passerines. *Evolution* **59**, 2669–2677.
- SOL, D., TIMMERMANS, S. & LEFEBVRE, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour* **63**, 495–502.
- SØRENSEN, J. G., NORRY, F. M., SCANNAPIECO, A. C. & LOESCHCKE, V. (2005). Altitudinal variation for stress resistance traits and thermal adaptation in adult *Drosophila buzzatii* from the New World. *Journal of Evolutionary Biology* **18**, 829–837.
- SORENSEN, M. D., SEFC, K. M., PAYNE, R. B. (2003). Speciation by host switch in brood parasitic indigobirds. *Nature* **424**, 928–931.
- STAMPS, J. A. (1988). Conspecific attraction and aggregation in a territorial species. *American Naturalist* **131**, 329–347.
- STAMPS, J. A. (1991). The effect of conspecifics on habitat selection in territorial species. *Behavioural Ecology and Sociobiology* **28**, 29–36.
- ST-CYR, J., DEROME, N. & BERNATCHEZ, L. (2008). The transcriptomics of life-history trade-offs in whitefish species pairs (*Coregonus* sp.). *Molecular Ecology* **17**, 1850–1870.
- STEARNS, S. C. (1992). *The evolution of life histories*. Oxford University Press, Oxford.
- STEFANESCU, C., CARNICER, J. & PEÑUELAS, J. (2011a). Determinants of species richness in generalist and specialists Mediterranean butterflies: the negative synergistic forces of climate and habitat change. *Ecography* **34**, 353–363.
- STEFANESCU, C., TORRE, I., JUBANY, J. & PÁRAMO, F. (2011b). Recent trends in butterfly populations from north-east Spain and Andorra in the light of habitat and climate change. *Journal of Insect Conservation* **15**, 83–93.
- STEPHENS, P. R. & SUTHERLAND, W. J. (1999). Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution* **14**, 401–405.
- STEPHENS, P. R. & WIENS, J. J. (2003). Explaining species richness from continents to communities: the time-for-speciation effect in Emydid turtles. *American Naturalist* **161**, 112–128.
- STEVENS, V. M., TURLURE, C. & BAGUETTE, M. (2010). A meta-analysis of dispersal in butterflies. *Biological Reviews* **85**, 625–642.
- STINGHCOMBE, J. R. & HOEKSTRA, H. E. (2008). Combining population genomics and quantitative genetics: finding the genes underlying ecological important traits. *Heredity* **100**, 158–170.
- STINGHCOMBE, J. R., WEINING, C., UNGERER, M., OLSEN, K. M., MAYS, C., HALLDORSÓTTIR, S. S., PURUGGANAN, M. D. & SCHMITT, J. (2004). A latitudinal cline in flowering time in *Arabidopsis thaliana* modulated by the flowering time gene FRIGIDA. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 4712–4717.
- STORZ, J. F. & WHEAT, C. W. (2010). Integrating evolutionary and functional approaches to infer adaptation at specific loci. *Evolution* **64**, 2489–2509.
- STREELMAN, J. T. & DANLEY, P. D. (2003). The stages of vertebrate evolutionary radiation. *Trends in Ecology and Evolution* **18**, 126–131.
- STUDDS, C. E., KYSER, T. K. & MARRA, P. P. (2008). Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proceedings of National Academy of Sciences* **105**, 2929–2933.
- SUTCLIFFE, O. L., THOMAS, C. D. & MOSS, D. (1996). Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology* **65**, 85–95.
- SWENSON, N. G. & HOWARD, D. J. (2005). Clustering of contact zones, hybrid zones, and phylogeographic breaks in North America. *American Naturalist* **166**, 581–590.



- TELLERÍA, J. L., RAMÍREZ, A. & PÉREZ-TRIS, J. (2008). Fruit tracking between sites and years by birds in Mediterranean wintering grounds. *Ecography* **31**, 388–388.
- TIEWS, J., BROSE, U., GRIMM, V., TIELBORGER, K., WICHMANN, M. C., SCHWAGER, M. & JELTSCH, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92.
- THOMAS, C. D., BODSWORTH, E. J., WILSON, R. J., SIMMONS, A. D., DAVIES, Z. G., MUSCHE, M. & CONRADT, L. (2001). Ecological and evolutionary processes at expanding range margins. *Nature* **411**, 577–581.
- THOMAS, J. A., MOSS, D. & POLLARD, E. (1994). Increased fluctuations of butterfly populations towards the northern edges of species' ranges. *Ecography* **17**, 215–220.
- THOMPSON, J. N. (2005). *The geographical mosaic of coevolution*. The University of Chicago Press, Chicago.
- THOMSON, R. L., FORSMAN, J. T., SARDÀ-PALOMERA, F. & MÖNKKÖNEN, M. (2006). Fear factor: prey habitat selection and its consequences in a predation risk landscape. *Ecography* **29**, 507–514.
- THULLER, W., LAVOREL, S., MIDGLEY, G., LAVERGNE, S. & REBELO, T. (2004). Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. *Ecology* **85**, 1688–1699.
- TING, S., HARTLEY, S. & BURNS, K. C. (2008). Global patterns in fruiting seasons. *Global Ecology and Biogeography* **17**, 648–657.
- TOEWS, D. P. L. & IRWIN, D. E. (2008). Cryptic speciation in a Holarctic passerine revealed by genetic and bioacoustic analyses. *Molecular Ecology* **17**, 2691–2705.
- TSONG, A., TUCH, B., LI, H. & JOHNSON, A. (2006). Evolution of alternative transcriptional circuits with identical logic. *Nature* **443**, 415–420.
- TURNER, J. R. G., LENNON, J. J. & LAWRENSON, J. A. (1988). British bird species distributions and the energy theory. *Nature* **335**, 539–541.
- URBAN, M. C., LEIBOLD, M. A., AMARASEKARE, P., DE MEESTER, L., GOMULKIEWICZ, R., HOCHBERG, M. E., KLAUSMEIER, C. A., LOEUILLE, N., DE MAZANCOURT, C., NORBERG, J., PANTEL, J. H., STRAUSS, S. Y., VELLEND, M. & WADE, M. J. (2008). The evolutionary ecology of metacommunities. *Trends in Ecology and Evolution* **23**, 311–317.
- URBAN, M. C. & SKELLY, D. K. (2006). Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology* **87**, 1616–1626.
- VAMOSI, J. C. & VAMOSI, S. M. (2010). Key innovations within a geographical context in flowering plants: towards resolving Darwin's abominable mystery. *Ecology Letters* **13**, 1270–1279.
- VAN BOCXLAER, I., LOADER, S. P., ROELANTS, K., BIJU, S. D., MENEGON, M. & BOSSUYT, F. (2010). Gradual adaptation toward a range-expansion phenotype initiated the global radiation of toads. *Science* **327**, 679–682.
- VAN DOORN, G. S., EDELAAR, P. & WEISSING, F. J. (2009). On the origin of species by natural and sexual selection. *Science* **326**, 1704–1707.
- VAN RENSBURG, B. J., CHOWN, S. L. & GASTON, K. J. (2002). Species richness, environmental correlates, and spatial scale: a test using South African birds. *American Naturalist* **159**, 566–577.
- VASEMÄGI, A. & PRIMMER, C. R. (2005). Challenges for identifying genetic variation: the promise of combining complementary research strategies. *Molecular Ecology* **14**, 3623–3642.
- VELLEND, M. (2005). Species diversity and genetic diversity: parallel processes and correlated patterns. *American Naturalist* **166**, 199–215.
- VIEIRA, F. G. & ROZAS, J. (2011). Comparative genomics of the Odorant-Binding and Chemosensory Protein gene families across the Arthropoda: origin and evolutionary history of the chemosensory system. *Genome Biology and Evolution* **3**, on line early.
- VIOLLE, C., NAVAS, M., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. & GARNIER, E. (2007). Let the concept of trait be functional! *Oikos* **116**, 882–892.
- VISSER, M., SCHAPER, S., VAN OERS, K., CARO, S. & HELM, B. (2010). Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **365**, 3113–3127.
- VITT, L. J. & PIANKA, E. R. (2005). Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 7877–7881.
- WATT, W. B. (1983). Adaptation at specific loci. II. Demographic and biochemical elements in the maintenance of the *Colias* PGI polymorphism. *Genetics* **103**, 691–724.
- WEBB, C. O., ACKERLY, D. D., MCPEEK, M. A. & DONOGHUE, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33**, 475–505.
- WEIR, J. T. (2006). Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution* **60**, 842–855.
- WEIR, J. T. & SCHLUTER, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315**, 1574–1576.
- WHEAT, C. W., FESCEMYER, H. W., KVIST, J., TAS, E., VERA, J. C., FRILANDER, M. J., HANSKI, I. & MARDEN, J. H. (2011). Functional genomics of life history variation in a butterfly metapopulation. *Molecular Ecology* **20**, 1813–1828.
- WHEAT, C. W., VOGEL, H., WITTSTOCK, U., BRABY, M., UNDERWOOD, D. & MITCHELL-OLDS, T. (2007). The genetic basis of a plant-insect coevolutionary key innovation. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 20427–20431.
- WIENS, J. J. (2007). Global patterns of diversification and species richness in amphibians. *American Naturalist* **170**, S86–S105.
- WIENS, J. J. & DONOGHUE, M. J. (2004). Historical biogeography, ecology, and species richness. *Trends in Ecology and Evolution* **19**, 639–644.
- WIENS, J. J. & GRAHAM, C. H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology and Systematics* **36**, 519–539.
- WIENS, J. J., PYRON, R. A. & MOEN, D. S. (2011). Phylogenetic origins of local-scale diversity patterns and the causes of Amazonian megadiversity. *Ecology Letters* **14**, 643–652.
- WIKELSKI, M., MARTIN, L. B., ROBINSON, M. T., ROBINSON, N. D., SCHEUERLEIN, A., HELM, B., HAU, M. & GWINNER, E. (2008). Avian circannual clocks: Adaptive significance and possible proximate control by energy turnover. *Philosophical Transactions of the Royal Society London B-Biological Sciences* **363**, 411–423.
- WILLI, Y. & HOFFMANN, A. A. (2009). Demographic factors and genetic variation influence population persistence under environmental change. *Journal of Evolutionary Biology* **22**, 124–133.
- WOLF, J. B. W., LINDELL, J. & BACKSTRÖM, N. (2010). Speciation genetics: current status and evolving approaches. *Philosophical Transactions of the Royal Society of London B* **365**, 1717–1733.
- WRIGHT, I. J., REICH, P. B., WESTOBY, M., ACKERLY, D. D., BARUCH, Z., BONGERS, F., CAVENDER-BARES, J., CHAPIN, T., CORNELISSEN, J. H., DIEMER, M., FLEXAS, J., GARNIER, E., GROOM, P. K., GULIAS, J., HIROSAKA, K., LAMONT, B. B., LEE, T., LEE, W., LUSK, C., MIDGLEY, J. J., NAVAS, M. L., NIINEMETS, U., OLEKSYN, J., OSADA, N., POORTER, H., POOT, P., PRIOR, L., PYANKOV, V. I., ROUMET, C., THOMAS, S. C., TJOELKER, M. G., VENEKLAAS, E. J. & VILLAR, R. (2004). The worldwide leaf economics spectrum. *Nature* **428**, 821–827.
- WRIGHT, S., KEELING, J. & GILLMAN, L. (2006). The road from Santa Rosalia: a faster tempo of evolution in tropical climates. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 7718–7722.
- WU, P., JIANG, T. X., SUKSAWEANG, S., WIDELITZ, R. B. & CHUONG, C. M. (2004). Molecular shaping of the beak. *Science* **305**, 1465–1466.
- WYLES, J. S., KUNKEL, J. G. & WILSON, A. C. (1983). Birds, behaviour and anatomical evolution. *Proceedings of the National Academy of Sciences of the United States of America* **80**, 4394–4397.
- ZANG, H. (1980). The altitudinal influence on the population density and on the breeding biology of *Ficedula hypoleuca*, *Parus palustris*, *Parus major*, and *Parus ater* in the Harz Mountains (Germany). *Journal of Ornithology* **121**, 371–386.
- ZINK, R. M. & SLOWINSKI, J. B. (1995). Evidence from molecular systematics for decreased avian diversification in the Pleistocene epoch. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 5832–5835.
- ZOBEL, M., OTTO, R., LAANISTO, L., NARANJO-CIGALA, A., PÄRTEL, M. & FERNÁNDEZ-PALACIOS, J. M. (2011). The formation of species pools: historical habitat abundance affects current local diversity. *Global Ecology and Biogeography* **20**, 251–259.

## VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Appendix S1.** Supplementary methods and information for Fig. 3.

**Appendix S2.** Supplementary methods and information for Fig. 4.

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