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Climatic control of dispersal–ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient?

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ABSTRACT

We outline the potentially important role of dispersal in linking diversity patterns at different spatial and temporal scales, and the resulting potential to link hypotheses explaining macroscale patterns of diversity. We do this by proposing a possible mechanism linking climate to diversity patterns: we argue that climate, via effects of continuity of habitat availability in space and time, mediates a dispersal–ecological specialization trade-off at the metacommunity level that leads to latitudinal trends in dispersal ability, ecological specialization, range sizes, speciation and species richness, ultimately driving the latitudinal diversity gradient. This trade-off constitutes a possible mechanism for the strong macroscale correlation between climate and species richness that is consistent with recent ideas about niche conservatism and gradient lengths, as well as other leading hypotheses. We present an overview of predictions derived from our ideas. Of these, some have already been tested and supported and others are still open to debate or need testing. Together they provide a unique set of predictions that allows falsification.

Keywords

Climate, dispersal, latitudinal richness gradient, local adaptation, metacommunity, trade-off.

INTRODUCTION

The latitudinal diversity gradient – increasing species richness from the poles to the equator – is one of the best-known patterns in ecology. It is seen in a wide range of organisms, from the smallest invertebrates to mammals and trees, both terrestrial and marine (Hillebrand, 2004a,b). Exceptions tend to occur in relatively small taxonomic groups such as the Pinaceae (Stevens & Enquist, 1998). Despite much research on the gradient over 200 years and many proposed hypotheses (reviewed by Rohde, 1992, Willig *et al.*, 2003, and Mittelbach *et al.*, 2007), consensus about its cause(s) has not yet been achieved and no single mechanism is generally accepted.

Previous research suggests that some elements are indispensable in a general explanation of the latitudinal diversity gradient. In particular, many studies have revealed strong correlations between species richness patterns and climatic variables: mostly temperature and the availability of water. For a recent meta-analysis, see Field *et al.* (2009). Although these correlations are not necessarily causal and may just reflect covarying environmental factors (Ricklefs, 2004), they strongly suggest that climate should play a key role in any theory explaining the latitudinal diversity pattern (Whittaker *et al.*, 2001). It is also clear that biodiversity patterns result from processes acting at different spatial and temporal scales (Whittaker *et al.*, 2001), including both ongoing ecological influences and a long history of speciation–extinction dynamics (Ricklefs, 2004, 2007).

Key challenges in explaining the latitudinal diversity gradient are: (1) to integrate the essential elements of ecology, evolution and biogeography in a single framework that connects the different spatial and temporal scales, and (2) to identify the key driving mechanism(s). Here we draw attention to the potentially important role of dispersal, which is currently largely neglected in this discussion. Dispersal is a key process that connects the different spatial and temporal scales and links ecological and evolutionary processes. Based on the link between vagility and generalism (e.g. Dynesius & Jansson, 2000), we further suggest that a trade-off between dispersal ability and ecological specialization to local conditions, effective at a metacommunity level, is an important driver of large-scale diversity patterns. We argue that the position that organisms take along this trade-off gradient is mediated by climatic conditions. We therefore suggest that climate partially determines dispersal rates and their evolution

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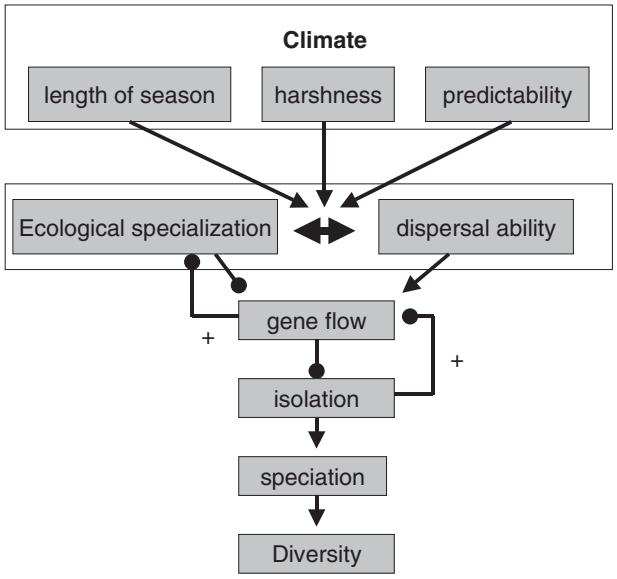

Figure 1 Visual representation of the climate-mediated dispersal–ecological specialization (CDES) trade-off and its effects on regional diversity. Single arrows indicate a stimulating impact (positive effect); a line ending in a circle indicates a restricting impact (negative effect). Double arrows indicate a trade-off. A '+' indicates a positive feedback that is discussed in the text.

in natural populations, which in turn affect rates of ecological specialization – and in the longer term, also speciation rates (Fig. 1). For convenience, we abbreviate 'climate-mediated dispersal–ecological specialization trade-off' to 'CDES trade-off' in the remainder of the paper.

Although the CDES trade-off has implications across many areas of ecology, our focus in this paper is on the implications for spatial patterns of biodiversity: we argue that it may be an important part of explaining the latitudinal diversity gradient. Integrating the trade-off with the metacommunity concept (Leibold *et al.*, 2004) and the climate-variability (e.g. Dynesius & Jansson, 2000) and time-for-speciation hypotheses (Wiens & Donoghue, 2004; Jablonski *et al.*, 2006) results in both a robust framework for explaining large-scale richness patterns and a series of predictions that can be tested.

The dispersal–ecological specialization trade-off

Dispersal connects populations and communities with surrounding populations and communities to create metapopulations and metacommunities, and thus plays a key role in determining patterns of local (alpha) and regional (gamma) diversity of taxa, as well as turnover (beta) diversity (Leibold *et al.*, 2004). Globally, the distribution of a taxon is determined by its dispersal history: its geographical starting point and the dispersal limitation imposed by both abiotic conditions and other taxa (Wiens & Donoghue, 2004). Because the movement of individuals is directly linked to the movement of the genes they carry, ecological processes influencing the movement of individuals have important evolutionary consequences, in the long term affecting speciation and biodiversity (Ronce *et al.*, 2001). Dispersal has been largely neglected in the literature on latitudinal diversity gradients, but is beginning to receive some attention (e.g. Roy & Goldberg, 2007).

The contribution of an individual organism to future generations determines its fitness. There are two major strategies for achieving high fitness at a regional scale. The first is to disperse readily, always moving away when relative performance declines and colonizing other habitats with (temporarily) higher survival probabilities for the offspring. The second is to remain in place and be ecologically specialized to the local conditions, including the abiotic environment and co-occurring organisms. Empirical evidence mostly comes from plants in the form of a trade-off between seed size and seed number (Jakobsson & Eriksson, 2003), and from the ranking of protozoan species according to their colonization abilities and their pairwise competitive interactions (Cadotte *et al.*, 2006). Although recently doubt has been cast over the commonness of this trade-off (Jakobsson & Eriksson, 2003), the local-adaptation trade-off between dispersal and competitive ability in organisms is generally accepted. This trade-off is intrinsic to the concept of the *r–K* continuum and related concepts of pioneer species versus species that dominate at later successional stages. The limited evidence available does indeed suggest that high dispersal is seldom successfully combined with stenotopic requirements (Marshall *et al.*, 2000). We argue that a broader version of this trade-off, opposing dispersal ability with traits that increase ecological adaptation to the local habitat, underlies the latitudinal diversity gradient.

Ecological specialization is expected to be negatively related to dispersal, for two main reasons. First, all else being equal, the probability of finding suitable conditions elsewhere declines with ecological specialization, selecting against dispersal. High dispersal rates allow rapid colonization and opportunistic exploitation of resources and are therefore typically associated with eurytropy, reduced chances of species niches disappearing and greater likelihood of their finding suitable habitat patches. Secondly, homogenization of the gene pool resulting from the genes the dispersing organisms carry may prevent adaptation to local conditions (Elena & Lenski, 2003). The balance between dispersal and the strength of selection for local resources determines the impact of gene flow on local ecological specialization (Case & Taper, 2000).

As a result, communities in habitats that greatly fluctuate in quality are largely composed of ecological generalists, good dispersers and opportunistic species. This ecological opportunism may be mediated either by genotypes supporting flexible adaptation to different conditions or by genetic versatility (diversity) of populations, and priority effects may play an important role in such systems (partly mediated by genetic versatility; De Meester *et al.*, 2002). Conversely, selection for ecological specialization results in communities composed of adapted species selected at a more local level. Such segregation of generalists and specialists in different communities has been observed for birds, with most species having a maximum abundance at a value of community specialization similar to their own level of specialization (Julliard *et al.*, 2006).

Climate mediates the dispersal–ecological specialization trade-off

Climate is a very complex phenomenon and several climatic characteristics may be relevant to its macroscale correlation with species richness (Lavers & Field, 2006). One characteristic that was first mentioned long ago, but with little recent attention, is the temporal variability of the climate (Fischer, 1960; Stevens, 1989; but see Dynesius & Jansson, 2000, and Hernández-Fernández & Vrba, 2005). Temporal climatic variability can be defined in terms of the magnitude and periodicity of fluctuations in key elements of climate, such as temperature and precipitation, at a range of temporal scales. Key components of climatic variability are seasonality, harshness, predictability and the length of the annual favourable period. The range of the key climatic elements is associated with the seasonality and the extreme values constitute the 'harshness' of a climate. Predictability is the consistency of climatic conditions between years, in terms of both mean values and seasonal fluctuations. The favourable period can be defined as the period of the year allowing growth and reproduction. We refer to climates with little variability as 'stable' climates. Towards higher latitudes, climatic conditions tend to become harsher and less predictable and there are shorter favourable periods (Stevens, 1989; Vázquez & Stevens, 2004; Pawar, 2005). These increasingly unfavourable climatic conditions for biota from the equator to the poles increase stress (Grime, 1979; Brown & Lomolino, 1998), thus tending to increase mortality and variation in population and community densities (e.g. Hansson & Henttonen, 1998), though little empirical evidence on changes in population fluctuations with environmental stochasticity is available at large spatial scales.

High temporal variability of the environment selects for increased dispersal ability (Gandon & Michalakis, 2001), which allows organisms to track their preferred habitat better. Three main mechanisms drive this selection. First, predictable temporal variation, such as seasonal fluctuations, may select for seasonal migration, which is obviously linked to dispersal capacity. A good example is the long-distance seasonal migration of birds and other organisms (Berthold, 1994). The long, cold winter nearer to the poles is a major cause of death for many organisms. The mortality risk is so high that it is worth risking the highly dangerous journey to more favourable climates to survive the unfavourable period. From higher to lower latitudes, smaller proportions of the biota migrate seasonally, with fewer long-distance travellers (Berthold, 1994). On a longer time-scale, plant diversity in Europe over the last 320,000 years is known to correlate negatively with climatic variability of that period (Willis *et al.*, 2007). The mechanism behind such correlations remains unexplained. Secondly, temporal variability of the environment and disturbance causes more pronounced fluctuations in population density and increased probability of population extinction (Lande, 1993). Fluctuations in population density also increase the number of invasible patches, selecting for increased dispersal ability of organisms through higher colonization success (Gandon & Michalakis, 1999). Finally, an important mechanism for surviving temporarily unfavourable conditions is to produce resistant dormant stages such as seeds and spores that may survive harsh conditions. These dormant stages are known to promote dispersal (Figuerola *et al.*, 2005). Temporal variation in habitat quality (including non-seasonal disturbance) therefore promotes increased dispersal ability.

We suggest that the position that organisms occupy in relation to the adaptive trade-off between dispersal ability and ecological specialization to local conditions is in part driven by climate, via effects of continuity of habitat availability in time and space. By 'continuity of habitat availability' we mean the stable and little-altered presence of a habitat, allowing for organisms to adapt to it. The changing climate towards the poles should therefore result in lower average dispersal ability in the tropics than near the poles. Testing the dispersal ability of organisms is a difficult matter, and we are unaware of any tests of this prediction. Similarly, evidence for or against ecological specialization being greater in tropical regions is limited. One relevant study (Novotny *et al.*, 2006) suggests that food resources are not more finely partitioned among folivorous insects (chrysomelid beetles) in tropical than in temperate forests, based on the diversity of the host plants used. However, as plant diversity increased sevenfold from the temperate to the tropical study sites, it may be that ecological specialization did actually increase, if the relative abundance and representation of host plants in an area are taken into account.

Since dispersal ability is related to distribution, and the geographic range of species reflects the interaction of limiting environmental conditions (niche width) and dispersal–extinction dynamics (Brown *et al.*, 1996) over time, reduced dispersal ability should tend to lead to reduced range size. A weak, indirect prediction is therefore that, other things being equal, the mean range size of species should increase from the equator to the poles. This pattern, known as Rapoport's rule (Stevens, 1989), has mixed support in the literature, with recent evidence for plants (Qian & Ricklefs, 2007), lichens and fungi (Wiens & Donoghue, 2004) supporting it, but with other studies failing to find significant latitudinal trends (e.g. Ruggiero & Werenkraut, 2007).

The best evidence we know of to substantiate the expected lower average dispersal ability of organisms towards the equator is in the population-genetics literature. Several studies have found that genetic divergence across space is greater at lower latitudes (e.g. Eo *et al.*, 2008). Reduced gene flow and greater isolation by distance are documented in tropical insect (Aulard *et al.*, 2002) and plant (Thomas *et al.*, 2002) populations, suggesting reduced dispersal distances in the tropics.

Climate, dispersal and speciation

If climate – particularly the harshness, predictability and length of the favourable season – affects the dispersal ability of organisms and their evolution in natural populations, it may also affect natural speciation rates. Within regions, the higher dispersal abilities and associated increased movement of individuals between populations in more temporally variable

environments make geographic isolation, probably the most important speciation process (Rosenzweig, 1995), less likely. When populations are not easily isolated, adaptive divergence and ultimately speciation rates tend to be relatively low (Garant *et al.*, 2007). The reduced dispersal capacities of most specialist species (Brouat *et al.*, 2004) increase the likelihood of dispersal limitation (Hubbell *et al.*, 1999), isolation of (meta)populations and ultimately speciation. This should result in higher speciation rates in the tropics than at higher latitudes.

The expected higher speciation rates in less temporally variable climates may be reinforced by positive feedback. This is because more specialized species, confined to narrower niches (specific environmental conditions), tend to be less able to readapt to new conditions, resulting in increased specialization to local conditions (Elena & Sanjuán, 2003). Ecological specialization, low dispersal ability and the increased isolation resulting from low dispersal ability are self-reinforcing mechanisms that may further enhance speciation rates in the tropics (Fig. 1). In the long-term this will result in higher gamma diversity (latitudinal diversity gradient). Thus the combination of ecological specialization and low dispersal rates provides a possible mechanism for the evolutionary-rates hypothesis, which is often invoked to explain the latitudinal diversity gradient (Rohde, 1992) and has received recent support (Allen *et al.*, 2006).

Towards a general framework

Our primary aim is to point to the potentially important role of dispersal in explaining the latitudinal diversity gradient and linking existing hypotheses. We do this by presenting an explanatory framework, centred around metacommunity processes and a CDES trade-off, to help explain the global richness patterns. In this framework we incorporate a shift from selection for relatively high dispersal rates and associated ecological generalism at higher latitudes, to selection for lower average dispersal capacity and associated local ecological specialization at lower latitudes. We suggest that this shift is climatically controlled, via continuity of habitat availability in time and space, meaning that species richness and various other phenomena (see corollary predictions below) should covary with climate. Thus we provide a mechanism that can explain why both species richness and speciation rates are higher in the tropics.

The central element in this framework is the CDES trade-off, which is driven by contemporary climatic conditions. Together with local habitat patch characteristics (both abiotic and biotic) and regional metacommunity structure (e.g. number and connectivity of patches), the resulting vagility of organisms will influence the distribution of genotypes and/or species in a metacommunity (Leibold *et al.*, 2004). As long as the climatic conditions remain similar, the resulting exchange of organisms and their genes is expected to result in a stable speciation rate (*sensu* Dynesius & Jansson, 2000) in the region. As argued earlier, this speciation rate is expected to be higher in more stable climates (e.g. near the equator) than in harsher and more variable climates (e.g. at higher latitudes). On a longer time-scale, climatic oscillations, such as Milankovitch oscillations, change the environmental conditions and we expect them to have two major effects on diversity in a region. First, climatic variations cause large-scale extinctions that disproportionately remove the more specialized organisms, tending to leave the more vagile and generalist species. This outcome is predicted by the ORD hypothesis (orbitally forced species range dynamics; Dynesius & Jansson, 2000). Secondly, based on our reasoning, climatic oscillations shift the balance in the dispersal–local ecological specialization trade-off, with clear consequences for the vagility of organisms and the exchange of individuals and genes, linking ecological and evolutionary time-scales. The intensity of, and the time between, climatic oscillations constrain the regional diversity: this is the essence of the time hypothesis (Pianka, 2000), which suggests that time for speciation is what limits species richness.

These considerations lead us to argue that dispersal links scales in both time and space: local community species richness with macroscale species-richness patterns, and ecological and evolutionary time-scales. This is why it can link together and elucidate the roles of existing hypotheses for latitudinal diversity gradients.

Core and corollary predictions

Conclusive testing of ideas related to the latitudinal diversity gradient is not easy because of the large number of hypotheses and the difficulty of experimental manipulation (Currie *et al.*, 2004; see also Hawkins *et al.*, 2007, and accompanying forum). We therefore outline a series of core and corollary predictions that, together, can be tested to build up evidence for or against our ideas. The proposed CDES trade-off has three main components that are expected to be present in any system, and we predict that these should be detectable, if not dominant, where there is sufficient variation in the key variables (core predictions).

1. *Trade-off between dispersal ability and ecological specialization.* We expect the presence of a trade-off between dispersal ability and ecological specialization. Ecological specialization can be defined as the competitive edge an individual has over another in a specific environment, considering both biotic and abiotic factors.

2. *Dispersal distance.* We expect an average longer dispersal distance of species in populations occurring in more climatically variable environments (e.g. closer to the poles).

3. *Speciation.* The CDES trade-off predicts (i) higher speciation rates in environmentally more stable areas. Specifically, we predict a monotonic negative correlation between climatic variability and speciation rates. This pattern is also predicted by both the metabolic theory of ecology (Allen *et al.*, 2006) and the biotic interaction hypothesis (Schemske, 2002). Our framework also predicts (ii) higher levels of endemism, especially continental endemism, in more stable environments. Whereas Whittaker *et al.* (2001) suggest that patterns of endemism can be explained mainly by historical contingency and not climate, our ideas suggest that climate may have more of an influence on endemism than previously thought. Small geographic range in a species can result because it has only recently evolved from a

small founder population (neo-endemism), because it has failed to spread from its area of evolution despite a long time period, because it has become extinct across much of its former range (palaeo-endemism) or a combination of these. The CDES trade-off predicts that these scenarios are more likely to occur in more stable environments, other things being equal (failure to spread is obviously often due to strong barriers to dispersal, such as being on isolated islands).

Although equilibrium is not required by our framework, the longer the climatic conditions remain broadly consistent the stronger we expect our predictions to be. As noted above, the very limited empirical data provide mixed support for these core predictions, but these data do not come from studies designed to test our predictions. To determine the empirical support for our propositions, there is a clear need for focused studies, on broad spatial scales and on a range of taxonomic groups.

In addition to the core predictions, the proposed CDES trade-off leads to a series of testable corollary predictions (i.e. phenomena consequent to our core ideas, which should also be found if our core ideas are true; Currie *et al.*, 2004). We set these out, non-exhaustively, as broad predictions, with specific ones numbered for each. As is the norm for attempts to explain the latitudinal diversity gradient, few if any of the individual predictions (core and/or corollary) are unique to our framework. However, when combined they represent unique sets of predictions. Further, some are stronger predictions than others (again the norm), but they are testable, at least in principle, and wholesale falsification of the predictions, especially the stronger ones, allows rejection of our framework.

1. Positioning along the dispersal–local adaptation continuum in time and space

We have argued that species and populations tend to vary geographically in their position along the dispersal–local adaptation trade-off, because of the climatic regime. Based on the analogy between spatial and climatic gradients we expect (1) that this spatial pattern is mirrored by a similar pattern of positioning along the dispersal–local adaptation trade-off gradient over time, as climatic regimes change. Both in space and time, with a higher selection for dispersal, species and individuals are expected (2) to invest more in structures enhancing dispersal, such as the production of dormant stages, development of flight muscles in flying insects, etc., in more variable climates (e.g. towards the poles). We also predict (3) a gradient in parthenogenesis, with asexual organisms and species more abundant in more variable climates. The fact that there is ability to reproduce without a partner increases colonization ability and thus effective dispersal in asexual organisms, while the absence of recombination strongly reduces their capacity for local adaptation (Lynch, 1987). This pattern is also predicted by the geographic parthenogenesis hypothesis (Haag & Ebert, 2004), which suggests that high-latitude populations are more likely to be susceptible to population bottlenecks, the negative effects of which are more pronounced in sexually reproducing species than in those that reproduce asexually.

2. Extinction rates and climatic changes

Based on the higher resilience of regionally adapted generalist species, the CDES trade-off framework predicts that, following a comparable catastrophic environmental change, (1) more extinctions occur in climatically more stable areas, with (2) the narrow-ranged species of stable climates wiped out disproportionately. Higher extinction rates in the tropics are also predicted by some dynamic mid-domain models (e.g. Arita & Vázquez-Domínguez, 2008). After the environmental changes, (re)positioning along the dispersal–local adaptation trade-off stabilizes the speciation rate and the remaining (generalist) species will start a new process of specialization. With higher expected average speciation and extinction rates in the tropics, the CDES trade-off predicts (3) a greater long-term turnover of species through time in the tropics. If extinctions are mainly caused by major perturbations (e.g. major climate changes), we expect speciation rates to be greater than extinction rates during 'normal' conditions, especially in the tropics, and therefore that (4) overall species numbers will increase through time in the absence of major perturbations.

3. Latitudinal gradient in metacommunity characteristics and dynamics

Selection for high dispersal rates is expected to result in (1) individuals and species that are selected for at a larger spatial scale (i.e. a larger effective recruitment area) with increasing latitudes. Thus our framework also predicts that (2) the effective size of the 'local' and 'regional' scales, as often used in metapopulation and metacommunity research (Leibold *et al.*, 2004), decreases towards the equator. This hypothesis can be tested by quantifying the dispersal dynamics in metacommunities at different latitudinal scales. In the gradient of dispersal limitation (patch dynamics ↔ species sorting ↔ mass effects; Leibold *et al.*, 2004), we expect (3) a shift from higher dispersal limitation near the equator towards more species sorting and mass effects in metacommunities at higher latitudes. This prediction could be tested by determining the relative importance of local and regional processes in similar habitat patches that occur in comparable configurations at lower and higher latitudes.

Linking the CDES to other ideas

We finish by briefly examining how our focus on the climate-mediated shift along the dispersal–local adaptation trade-off relates to selected recent ideas on the latitudinal diversity gradient.

In a classic paper revisited in Ghalambor *et al.* (2006), Janzen (1967) presented a climatic–physiological model predicting that tropical mountain passes would be more effective barriers to organismal dispersal than would temperate-zone passes of equivalent altitude.

The rationale is that the range of environmental variation in the more stable climates (particularly in terms of temperature) of the tropics is much less than in the temperate zones, resulting

in narrow physiological tolerances of the tropical organisms. This creates higher dispersal costs of crossing environmental barriers and results in smaller ranges, reduced gene flow between populations and increased allopatric speciation. The hypothesis fits well with our ideas, which add a new element: the CDES trade-off. While Janzen discussed a speciation mechanism that relates to crossing environmental (climatic) gradients, the CDES trade-off suggests that there should be lower dispersal within areas with similar average but more constant climate.

Stevens (1989) suggested that greater geographic ranges of species close to the poles result from broad environmental tolerance, again a consequence of exposure to more variable environments. This idea is similar to ours, but Stevens did not make the same link with dispersal, and presented no speciation mechanism. His brief mention of dispersal was in comparing species with similar dispersal capacities at different latitudes: how this can lead to more 'misplaced' organisms, out of their preferred habitat. He hypothesized that the resulting higher rate of 'accidentals' in the tropics inflates the diversity and inhibits competitive exclusion.

Lavers & Field (2006) proposed another mechanism that may account for the strong correlations between some climate variables and species richness. They argued that greater inputs of resources such as water and light in terms of radiant energy per surface area – as found in much of the tropics – allow the existence of more combinations of different levels of these resources, offering greater opportunity for niche differentiation, increased specialization and speciation, if there is sufficient time and habitat volume available. This idea may be complementary to the one outlined here, and the combination of greater opportunities for local niche differentiation among species and climatic stability favouring specialist, poorly dispersing species represents a powerful set of mechanisms leading to higher alpha and gamma diversity in stable, favourable climates. It should also result in higher beta diversity because of greater dispersal limitation and finer subdivision of the environment (Qian & Ricklefs, 2007).

There is debate about whether the tropics should be viewed as evolutionary 'cradles' or 'museums' of diversity (e.g. Jablonski *et al.*, 2006), or perhaps both at the same time (McKenna & Farrell, 2006). Jablonski *et al.* (2006) described a simple, two-box model that contrasts the tropics (T) and the extra-tropics (E) in terms of speciation ('origination': O_T vs. O_E), global extinction (E_T vs. E_E) and changes in geographical distribution ('immigration': I_T vs. I_E). They used this model to compare several theoretical models that differ in the relative importance of these processes. The CDES predicts that extinction rates depend in large part on the nature, frequency and intensity of climatic changes, while the length of the period in between significant climatic changes should affect opportunities for speciation, partly determining the impact of specific climate changes. Given that there are many more species in the tropics, and that the selection for vagility and generalism at higher latitudes buffers climate oscillations effectively (Dynesius & Jansson, 2000), extinction rates are expected to be higher in the tropics than at higher latitudes. Yet, a strong latitudinal gradient can result, even in the absence of immigration into the tropics, because of the much higher speciation rates (Fig. 1). The CDES thus suggests that $O_T > O_E$, but also that, most of the time, $E_T > E_E$. The main difference between this and the 'out of the tropics' model of Jablonski *et al.* (2006) is that their model has $E_T < E_E$, while we predict $E_T > E_E$, a scenario that they mention only as an aside, with reference to Stenseth (1984). Using Stebbin's metaphor, we therefore argue that, much of the time, the tropics are a cradle but not a museum (rather, a mortuary), while Jablonski *et al.* argue that the tropics are both a cradle and a museum.

However, global history should not be ignored, and there have been times when major changes have occurred in the world's climate system. One such change occurred in the transition from the Palaeogene to the Neogene, which was associated with global cooling that culminated in the Pleistocene. In the much warmer world of the Palaeogene, the latitudinal temperature gradient was much less pronounced and conditions globally were much more like the present-day tropics than the present-day higher latitudes (Behrensmeyer *et al.*, 1992). Hawkins *et al.* (2006) suggested that many existing warm-adapted clades were eliminated by these changes, especially outside the tropics, to be replaced by newer clades that evolved to cope with the new, colder and less stable conditions. This is exactly as expected from the CDES, as is the suggestion by Hawkins *et al.* (2006) that there has also been dispersal limitation of highly derived clades. During the major climatic change from the Palaeogene to the Neogene, $E_T < E_E$ is therefore expected from CDES.

The niche conservatism hypothesis (Wiens & Donoghue, 2004) can be viewed as an extension of the time hypothesis (Pianka, 2000), and in essence is another version of the climate variability hypothesis, suggesting that the richest areas are those whose environmental conditions most closely match past conditions, experiencing the least climatic variation. These hypotheses explain differences between areas mainly based on the amount of time available for specialization and speciation of the occurring organisms. The effect of long-term climatic oscillations is different, and provides an additional element affecting speciation and extinction rates in particular conditions. The positive effect of climatic continuity on the number of specialized species may combine with the effects of the contemporary climate that we outline here such that, starting from the same number of species and given the same time under a given climatic regime, there will be fewer species in more temporally variable, climatically harsher areas. A tendency towards niche conservatism is likely to enhance extinction rates associated with major environmental changes (see previous paragraph).

The relative contributions of these all elements to macroscale species richness patterns are difficult to predict, making our corollary predictions particularly important for testing and falsification.

CONCLUSION

By presenting a framework and speciation mechanism underlying the latitudinal diversity gradient, we have tried to point out

the potentially important role of dispersal and metacommunity processes in explaining global biodiversity patterns: dispersal is a key anchor point linking other processes that, in combination, determine these gradients. We know surprisingly little about the role of dispersal in determining large-scale diversity patterns, and in the rapidly changing world in which we live it is essential to have a good understanding of how the two are linked.

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BIOSKETCHES

The main research interests of **Merlijn Jocque** are diversity patterns in time and space, with particular interest in metacommunity dynamics and the process of dispersal. **Richard Field's** main interests are biogeography, macroecology and plant ecology, with particular focus on biodiversity and the forces that structure ecological communities. The research interests of **Luc De Meester** focus on evolutionary ecology, reconstructing evolutionary responses from the archive provided by layered dormant egg banks, and the interface between evolutionary and ecological processes at the metacommunity level ('evolving metacommunities' concept). Author contributions: M.J. conceived the initial idea; M.J, R.F. and L.D.M. contributed equally to the further development of the idea; M.J. and R.F. wrote the manuscript, with input from L.D.M. and L.B.

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