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REVIEW AND SYNTHESIS

Metacommunity speciation models and their implications for diversification theory

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Abstract

The emergence of new frameworks combining evolutionary and ecological dynamics in communities opens new perspectives on the study of speciation. By acknowledging the relative contribution of local and regional dynamics in shaping the complexity of ecological communities, metacommunity theory sheds a new light on the mechanisms underlying the emergence of species. Three integrative frameworks have been proposed, involving neutral dynamics, niche theory, and life history trade-offs respectively. Here, we review these frameworks of metacommunity theory to emphasise that: (1) studies on speciation and community ecology have converged towards similar general principles by acknowledging the central role of dispersal in metacommunities dynamics, (2) considering the conditions of emergence and maintenance of new species in communities has given rise to new models of speciation embedded in the metacommunity theory, (3) studies of diversification have shifted from relating phylogenetic patterns to landscapes spatial and ecological characteristics towards integrative approaches that explicitly consider speciation in a mechanistic ecological framework. We highlight several challenges, in particular the need for a better integration of the eco-evolutionary consequences of dispersal and the need to increase our understanding on the relative rates of evolutionary and ecological changes in communities.

Keywords

Biotic interactions, dispersal, diversity-dependent diversification, ecological speciation, geographic speciation, habitat filtering, life history trade-offs, metacommunity dynamics, neutral models, species-sorting.

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INTRODUCTION

Biodiversity results from the diversification of species through space and time, which constitutes one of the most important biological processes. During the last two decades, the explosive growth of DNA sequence data has enabled the assembly of large-scale molecular phylogenies, providing an unprecedented level of resolution on the rate of species diversification (Phillimore & Price 2008, 1–5 in Appendix S1). This high resolution has considerably changed our views on diversification. Notably, it has been shown that the balance between the rates of speciation and extinction is not constant (McPeek 2008; Rabosky & Lovette 2008; Rabosky 2009; Rosindell & Phillimore 2011; Etienne & Haegeman 2012; Etienne & Rosindell 2012) and that not only plate tectonics and palaeoenvironments, but also interactions between local ecological dynamics and landscapes physical and ecological properties contribute in shaping large-scale patterns of diversification (Wiens & Donoghue 2004; Kisel *et al*. 2011; McInnes *et al*. 2011; Rosindell & Phillimore 2011, 6–7 in Appendix S1). From an evolutionary perspective, the formulation of an ecological model of speciation as an alternative to the traditional allopatric model has been a major advance in linking ecological and evolutionary processes (Losos *et al*. 1998; Schluter 1998, 2000a,b, 2001; Dieckmann *et al*. 2004; Gavrilets 2004; Nosil 2012). This approach has challenged our view of speciation by emphasising diversification on small spatial and temporal scales, in populations with ongoing gene flow between them, as a consequence of adaptive changes fostering reproductive isolation (Gavrilets & Losos 2009; Schluter 2009).

At the same time, community ecologists have also integrated the temporal and spatial scales at play during species diversification, particularly through metacommunity ecology (Leibold *et al*. 2004; Urban *et al*. 2008). They have disentangled the influence of species interactions and adaptation inside communities (*i.e*. local scale) and the influence of immigration of new species from outside the community (*i.e*. regional scale) on diversity dynamics (Ricklefs 1987; Hubbell 2001; Leibold *et al*. 2004; Logue *et al*. 2011, 8 in Appendix S1). This new theoretical framework recognises that the interplay between speciation and community dynamics is a direct consequence of the interdependence of mechanisms at local and regional scales (Urban *et al*. 2008; Vellend 2010). There is also

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a growing body of evidence that the spatial dynamics of metacommunities influence speciation by affecting both the opportunities of speciation and the persistence of incipient species (Gavrilets 2004; Gavrilets & Vose 2006; Kisel *et al.* 2011; Rosindell & Phillimore 2011; Desjardins-Proulx & Gravel 2012a, b; Nosil 2012).

While addressing the same processes, the integrative speciation models proposed by macro-evolutionary biologists and the new evolutionary paradigms arising from metacommunity theory have been developed independently and are currently scattered in the literature. Several attempts have been made to link ecological and evolutionary mechanisms into integrative theories of biodiversity. The ecological speciation and adaptive radiation models constitute two notable examples (Gavrilets 2004; Gavrilets & Losos 2009; Schluter 2009). These ecological hypotheses of speciation and diversification have opened new perspectives for integration of evolutionary and ecological sciences; however, they focus largely on niche theory and as such consider only part of the complexity of ecological communities (Hubbell 2001; Bonsall *et al.* 2004; Alonso *et al.* 2006; Etienne *et al.* 2007; Rosindell *et al.* 2010; Etienne & Rosindell 2012).

Recent studies on community ecology and diversification have shown that evolutionary dynamics (*i.e.* adaptation, speciation) overlap in space and time with ecological dynamics (*i.e.* dispersal, survival, coexistence) (McPeek 1996; Jansen & Mulder 1999; Gillespie 2004; Gavrilets & Vose 2006; McPeek 2008; Gavrilets & Losos 2009; Beardmore *et al.* 2011; Cornell 2013) creating a new theoretical framework (Etienne *et al.* 2007; Emerson & Gillespie 2008; Urban *et al.* 2008; Vellend 2010; Davies *et al.* 2011; Desjardins-Proulx & Gravel 2012a,b; Pillai & Guichard 2012; Ai *et al.* 2013). Here, we propose a synthesis that examines this paradigm at various scales of evolutionary (*i.e.* speciation vs. diversification) and ecological (*i.e.* local vs. regional) dynamics. We first detail the spatial and ecological framework embedded in metacommunity theory to emphasise how studies on speciation and ecological communities have converged towards similar general principles by acknowledging the central role of dispersal in metacommunities. Second, we present the three eco-evolutionary frameworks of the metacommunity theory (*i.e.* neutral, niche and life history trade-offs) and the new speciation models that have emerged from them. Third, we describe how studies of speciation and diversification have shifted from relating phylogenetic patterns to spatial and eco-evolutionary dynamics towards integrative approaches considering speciation in a metacommunity framework. Finally, we argue for a unified framework to study speciation and diversification and highlight several directions for future research.

METACOMMUNITY THEORY: A SPATIAL FRAMEWORK TO STUDY DISPERSAL AND SPECIES COEXISTENCE

A community is the collection of species occupying the same local patch. In practice, this broad definition covers a wide range of systems ranging from a subsample of continuous matrix (*e.g.* a 1 ha square plot of primary forest, a 100 m transect in a coral reef) to patches of habitat in fragmented landscapes (*e.g.* ponds, islands, host populations). The focus is on the scale where direct interactions among individuals occur vs. higher levels of spatial organisation at which dispersal and speciation prevail (Ricklefs 1987; Leibold *et al.* 2004). Within a community, species share space and resources according to their respective ecological requirements and, patch size, competitive interactions and niche space constitute a potential limit to the demographic expansion of the populations (Alonso *et al.* 2006, 9 in Appendix S1). At higher spatial scales of organisation, these communities are embedded in a network of communities linked by dispersal, called a metacommunity, where both local dynamics (*i.e.* biotic interactions, adaptation, patch size) and regional processes (*i.e.* dispersal, speciation) affect the dynamics of assembly and maintenance of communities (Hubbell 2001; Leibold *et al.* 2004, 8 in Appendix S1).

Metacommunity ecology has identified different mechanisms to explain species coexistence and diversity dynamics (Fig. 1). In its simplest form, a metacommunity can be represented by a local patch of which the composition varies neutrally according to stochastic fluctuations in demography and to immigration from a regional pool (Sale 1977; Hubbell 1979, 2001). The regional pool can be modelled either implicitly (Hubbell 2001) or explicitly (Economo & Keitt 2008, 2010; Rosindell & Phillimore 2011). In this neutral framework (Fig. 1A1), the only limit to the establishment of an immigrant is the space left available by the death of residents and the connectivity between the local patch and the regional pool. When the establishment of the immigrant is also limited by its biotic and abiotic environment and the limitations vary among species, species are 'sorted' among communities according to their ecological niches (Fig. 1B1). This model of resource-dependent survival, which corresponds to the traditional model of ecological niche originally formulated by Hutchinson (1959), was formalised as the species sorting metacommunity model (Leibold *et al.* 2004; Logue *et al.* 2011). This sorting can be mitigated when dispersal between communities is sufficiently high to counterbalance local competitive exclusion (the so-called 'mass effect' or 'source sink dynamics' (Schmida & Ellner 1984; Mouquet & Loreau 2002; Ai *et al.* 2013)). Furthermore, environmental perturbations and biotic interactions may jeopardise the survival of immigrants (Fig. 1C1) so that coexistence is only possible through the establishment of life history trade-offs between competitive ability and other traits such as colonisation ability or resistance to predation/perturbation (Hastings 1980; Calcagno *et al.* 2006, 10–12 in Appendix S1). To a certain extent, all these mechanisms can be positioned along a continuum between neutral and niche-based processes. All the non-neutral processes involve some form of trade-off between competitive abilities for different resources (*i.e.* species-sorting) or between life history traits (*i.e.* patch-dynamics).

The major contribution of metacommunity theory has been to disentangle the relative contribution of regional and local processes in regulating species richness within communities and to define a spatial framework to study multi-scale dynamics.

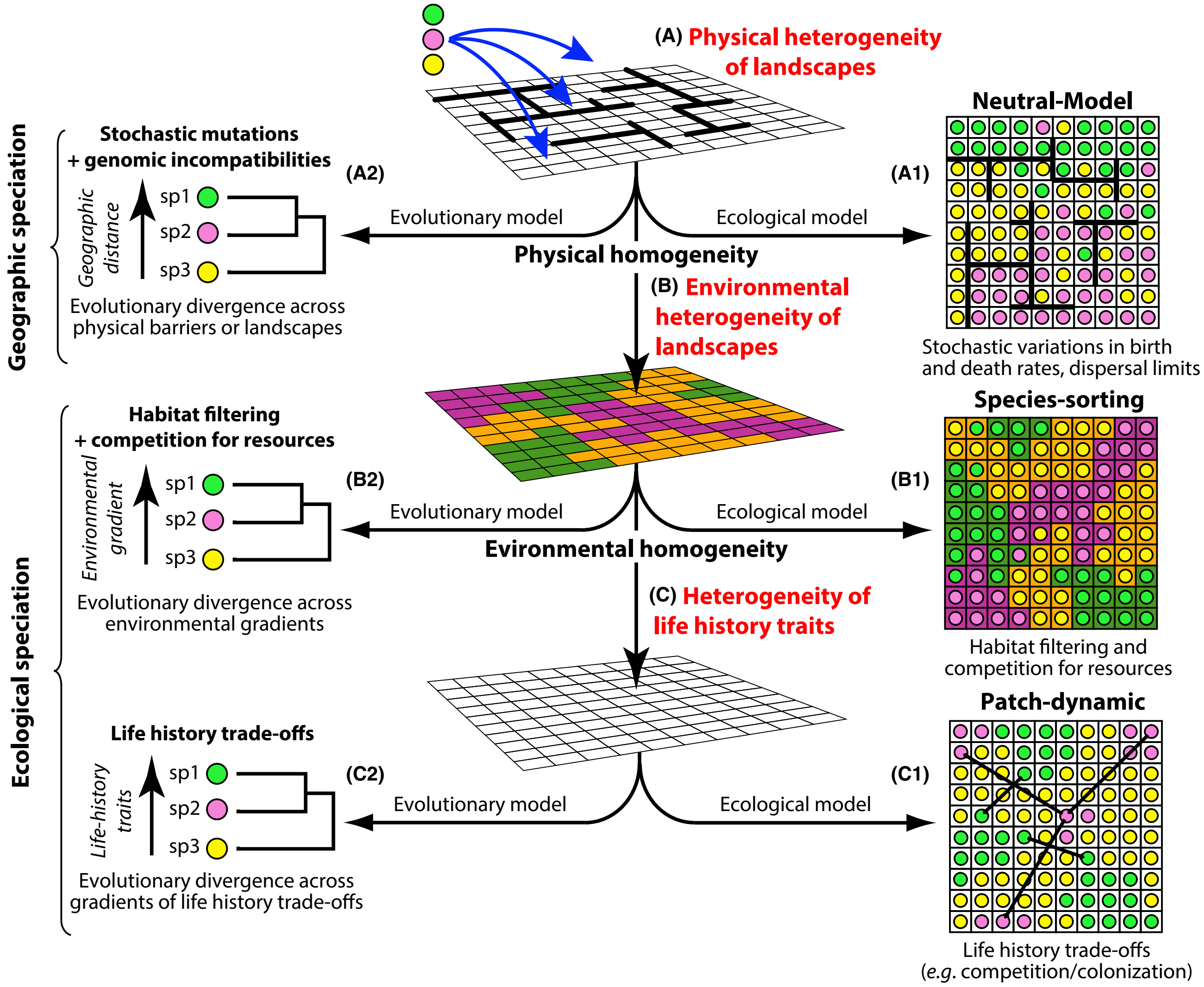

Figure 1 Landscape physical (A) and environmental (B) characteristics, life history traits (C) and associated conceptual frameworks in ecology and evolution. Species composition within and among communities can be determined by ecological and evolutionary consequences of demographic stochasticity (A), habitat filtering and competition for resources (B) and life history trade-offs (C). (A) In ecologically homogeneous landscapes hosting functionally equivalent species, species abundance in patches is determined by demographic stochasticity and genomic incompatibilities promoting reproductive isolation among populations. (B) In landscapes with environmental heterogeneity, species compete to use resources according to their niche and reproductive isolation results from adaptive shifts in traits defining ecological niches. (C) In landscapes where competitive interactions limit species coexistence on similar resources, species co-occurrence is driven by life history trade-off dynamics and reproductive isolation results from adaptive shifts in the trade-off space. Grids and circles in A1, B1 and C1 represent patches and populations, respectively. Arrows in C1 represent dispersal abilities.

ECOLOGICAL SPECIATION: LINKING ECOLOGICAL AND EVOLUTIONARY DYNAMICS

A species is a collection of interconnected populations maintaining their evolutionary cohesiveness through gene flow. Isolation mechanisms breaking gene flows among populations may emerge as a consequence of extrinsic (*e.g.* geographic speciation, disruptive natural selection) or intrinsic (*e.g.* chromosomal rearrangements) factors reducing gene flow through pre-mating (*e.g.* alternative mating behaviours) and/or post-mating (*e.g.* genomic incompatibilities) barriers (Coyne & Orr 2004; Dieckmann *et al.* 2004; Schluter 2009).

Allopatric speciation is the most straightforward model involving a physical barrier that disrupts gene flow (13 in Appendix S1). This model has dominated speciation studies in numerous systems for decades (Coyne & Orr 2004, 14–16 in Appendix S1) despite its pitfalls when applied to open systems (Dieckmann *et al.* 2004; Nosil 2012). Alternative models acting at different scales have been further proposed such as sympatric speciation (*i.e.* speciation occurring within the same region) and parapatric speciation (*i.e.* speciation occurring at the margin of a species' range distribution) (14–18 in Appendix S1). These alternatives improved our understanding of reproductive isolation, although, they considered separately mechanisms acting at regional (*e.g.* allopatric speciation and large-scale fragmentation of species range distribution) and local (*e.g.* sympatric speciation and local divergence through sexual selection) scales. As a consequence, dynamics at intermediate scales, such as population fragmentation in patchy landscapes, have remained out of the scope of speciation studies for decades (Dieckmann *et al.* 2004; Nosil 2012).

The development of an ecological theory of speciation has partly filled this gap by considering jointly the contribution of spatial and ecological constraints on speciation dynamics (Schluter 1998, 2001, 2009). Ecological speciation considers that adaptation to differential (environmental or biotic) conditions involves a tension between, on the one hand, ecological diversification through the rise of differentially adapted variants, and, on the other hand, genetic homogeneization by gene flow (Dieckmann *et al.* 2004). This departs from other models by considering the ontology of reproductive isolation as influenced by both local (*i.e.* diversifying selection and adaptation) and regional (*i.e.* dispersal and gene flow) scales. In this context, reproductive isolation may be (1) a by-product of adaptation and selection on other traits as a consequence of the accumulation of genomic incompatibilities and/or pleiotropic effects (Schluter 1998, 2000b, 2001; Turelli *et al.* 2001; Dieckmann *et al.* 2004; Gavrilets 2004; Nosil 2012, 19–21 in Appendix S1), (2) a direct consequence of selection acting on traits involved in both local adaptation and reproductive isolation, the so-called 'magic traits' (20–21 in Appendix S1). Both processes result from eco-evolutionary interactions occurring at local and regional scales, in a spatial and ecological framework very analogous to metacommunity theory (Leibold *et al.* 2004).

ECO-EVOLUTIONARY CONSEQUENCES OF DISPERSAL: TOWARDS COMMON PRINCIPLES IN SPECIATION AND COMMUNITY ECOLOGY STUDIES

In a metacommunity framework, dispersal is a central driver of diversity at both local and regional scales (Hubbell 2001; Economo & Keitt 2008, 22 in Appendix S1). When immigrants settle in new patches, they will (1) interact with residents and occupy empty space or replace residents leading to variations in community composition (*i.e.* ecological consequences), (2) potentially face new ecological conditions and pass favourable genes to their descendants leading to adaptive changes (*i.e.* evolutionary consequences). From an ecological perspective, dispersal drives ecological dynamics in communities by linking local and regional scales and this assumption is at the basis of the development of the metacommunity theory. From an evolutionary perspective, models of speciation with gene flow acknowledge the evolutionary consequence of dispersal and offer an evolutionary interpretation of the ecological dynamics linking local and regional scales (Fig. 1B2, C2) (Schluter 1998; Gavrilets 2004; Emerson & Gillespie 2008; Schluter 2009; Nosil 2012). Several syntheses have highlighted how metacommunity and ecological speciation models have converged by acknowledging the importance of the eco-evolutionary consequences of dispersal through local vs. regional dynamics (Dieckmann *et al.* 2004; Urban *et al.* 2008), however, these syntheses are currently scattered in the literature.

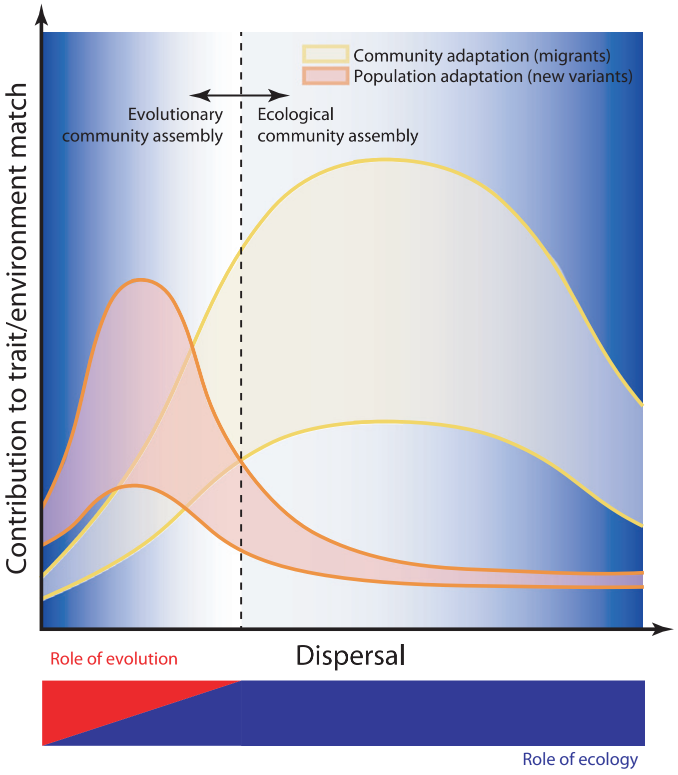

Figure 2 Relationships between the fit of traits to ecological resources and dispersal in populations and communities, and their consequences on community assembly. The fit of traits to resources can be increased through adaptive changes by mutation and selection in populations (i.e. evolution) or community assembly (i.e. species sorting). Dispersal increases species access to optimal patches and optimises the match between traits and resources until maladapted species persist through mass-effect dynamics. Similarly, mutation and natural selection optimise population traits in patches through the rise of new variants with increasing fitness until gene flow break advantageous allelic combinations through recombination. The match between traits and resources in populations and communities, however, will peak at different levels of dispersal, on a different order of magnitude and these differences are responsible for the relative contribution of ecological and evolutionary dynamics on community assembly and opportunities of speciation (Urban *et al.* 2008).

Dispersal promotes homogenisation of both gene pools and communities, but its effect on both community assembly and reproductive isolation may not be linear (Fig. 2). If considering adaptive changes in either a niche-based or trade-off perspective, dispersal brings novelty and thus increases diversity (both species richness and potential for local adaptation) but at the same time high dispersal rates will tend to homogenise the communities and reduce both species richness and local adaptation (Mouquet & Loreau 2002; Dieckmann *et al.* 2004; Vellend & Geber 2005; Urban *et al.* 2008, 23–24 in Appendix S1). Even if this duality of dispersal is a trend common to both the ecological and evolutionary perspectives, the levels at which dispersal homogenises the species and genes pools may differ (Urban *et al.* 2008). While a few migrants per generation are enough to homogenise neutral gene pools (25 in Appendix S1), mass-effects (homogenisation of species pools) require much higher rates of dispersal (Vellend 2005; Vellend & Geber 2005; Urban *et al.* 2008; Logue *et al.* 2011). The consequences of this duality and the discrepancy in the responses of speciation and community assembly to dispersal have been either predicted or observed in a wide range of metacommunity models, and predict in part the conditions for speciation in adaptive models. Bonsall *et al.* (2004), Jansen & Mulder (1999) and Mouquet *et al.* (2001) have described the same dynamics in cases of speciation arising through life history trade-off dynamics in patch-dynamics models.

The emerging pattern is that dispersal has either synergetic or antagonistic effects on speciation and community assembly depending on its relative importance compared to mechanisms at play in communities including stochastic fluctuations of demographic parameters and genetic drift (Fig. 1A1, A2), species-sorting and adaptive shifts (Fig. 1B1, B2), or biotic interactions and resulting adaptive shifts (Fig. 1C1, C2). By providing a spatial framework accounting for the complexity of the eco-evolutionary consequences of dispersal in populations and communities, the metacommunity emphasises the conditions for the emergence of new species in communities, accounting simultaneously for both populations (*i.e.* drift, gene flow, adaptation) and communities dynamics (*i.e.* random fluctuations, species-sorting, biotic interactions) (*e.g.* Fig. 2).

METACOMMUNITY SPECIATION MODELS

The rise of eco-evolutionary models of speciation and community dynamics, explicitly accounting for local vs. regional dynamics, paved the way for an integrative study of the impact of metacommunities dynamics on speciation opportunities. These new approaches not only shed a light on how we consider speciation but also provided a wider view on how speciation occurs in ecological communities, beyond the traditional geographical models (*i.e.* allopatry, sympatry and parapatry). New speciation models nested in the three frameworks of metacommunity theory have emerged built upon dispersal limitations and stochasticity (*i.e.* geographic speciation), the ecological niche (*i.e.* niche-based ecological speciation) and life history trade-offs (*i.e.* community-mediated ecological speciation). These models, and the new perspectives on speciation opened by the metacommunity perspective, are reviewed independently in the following subsections.

Model I – Ecological neutrality and geographic speciation in physically heterogeneous landscapes

A neutral model of species co-existence

In the 1970s, Sale (Sale 1977, 26–27 in Appendix S1) and Hubbell (Hubbell 1979) suggested that neutral dynamics might be sufficient to account for species abundance patterns in coral reef fish and tropical forest communities respectively. Neutrality has been a paradigm in population genetics for a long time (Kimura 1983) but it took more than two decades to percolate in community ecology until the book of Hubbell in 2001 (Hubbell 2001). Neutral models differ from the traditional niche-based models by their assumptions of ecological equivalence, ecological or neutral drift, zero-sum dynamics and the incorporation of speciation (Box 1). Notwithstanding the debate on the nature of species interactions (neutral or not), neutral models have brought back large-scale evolutionary processes into community ecology (Webb *et al.* 2002; Wiens & Donoghue 2004; Vellend 2010; Mouquet *et al.* 2012, 28 in Appendix S1). From an ecological perspective, the neutral theory is a dispersal-limited sampling theory built upon individual-based models (Alonso *et al.* 2006, 29 in Appendix S1). It enables confrontation to empirical data and provides a null model for community ecology that can be used to identify departures in empirical observations from its assumptions in a spatially explicit framework (30 in Appendix S1).

Box 1 The neutral paradigm

The Neutral Theory assumes that communities consist of functionally equivalent species (*i.e.* ecological equivalence) that saturate resources at all times such that the death of an individual will be immediately used by a new individual *i.e.* zero-sum dynamics (Hubbell 2001; Alonso *et al.* 2006). Given that species have similar birth and death rates, species abundances are driven by dispersal and both stochastic fluctuations in population demographic parameters and speciation probability is a function of species abundance (Etienne *et al.* 2007; Davies *et al.* 2011). This paradigm holds for landscapes with homogeneous ecological resources and hosting functionally equivalent species in which species abundance in patches are determined by dispersal limitation and demographic stochasticity (Hubbell 2001; Alonso *et al.* 2006; Economo & Keitt 2008, 2010; Rosindell & Phillimore 2011). In this context, reproductive isolation results from the accumulation of genomic incompatibilities among isolated populations due to limited gene flow *i.e.* geographic speciation (Desjardins-Proulx & Gravel 2012a,b) and community assembly is driven by dispersal limitations (bold lines in A1). After some time, a dynamic equilibrium between speciation and extinction is formed and species richness in communities reaches a stationary value as a function of dispersal and landscape geometry (Davies *et al.* 2011).

The neutral theory is based on the following initial assumptions:

(A1) Ecological equivalence (patches): all patches are ecologically equivalent and differ only in their connectance and centrality in the metacommunity (landscape ecology).
(A2) Ecological equivalence (species): interactions among species are assumed to be equivalent on an individual basis (community ecology).
(A3) Ecological or neutral drift (species): species abundances fluctuate and differ because of stochasticity in birth, death and dispersal (community ecology).
(A4) Zero-sum dynamics (communities): resources are saturated at all times. This implies that resources made available by the death of an individual will be immediately used by a new individual and providing resources are constant, local communities are of constant size (community ecology).
(A5) Speciation (regional pool) is a stochastic population process driven by species abundance, mutation and dispersal (Geographic speciation).

The neutral model: a metacommunity model of speciation

From an evolutionary perspective, the first neutral models were built upon individual-based speciation models assuming either point mutation speciation (*i.e.* a newly recruited individual is sampled at random and undergoes speciation) or random fission speciation (*i.e.* a species is divided into two at random) (Hubbell 2001), both being oversimplifications of speciation mechanisms (Coyne & Orr 2004; Dieckmann *et al.* 2004; Gavrilets 2004). Recently, Desjardins-Proulx & Gravel (2012a,b) proposed a population-based model of speciation with gene flow where reproductive isolation is caused by the progressive accumulation of incompatible alleles due to mutation and drift (Fig. 3A, B). The authors used graphs to control the spatial framework where the position of each community was defined by its centrality (*i.e.* closeness to the gravity centre) and connectance (*i.e.* number of connection with other communities) (Desjardins-Proulx & Gravel 2012a). In their simulations, the authors showed that peripheral communities with low connectance significantly accumulate more species through speciation than central communities with higher rates of immigration. In their system, however, Desjardins-Proulx & Gravel (2012a,b) found that speciation leads to more realistic estimates of species richness if mutations towards speciation are given a positive selective coefficient, which is a violation of the assumption of ecological equivalence. de Aguiar *et al.* (2009) obtained similar results by introducing some positive assortative mating in a stochastic metacommunity model while Melián *et al.* (2010) concluded that frequency-dependent selection leads to more species than neutral models. Later, Desjardins-Proulx & Gravel (2012b) modified their model by introducing differential allelic fitness for mating while ignoring individual fitness for dispersal. This is equivalent to assuming that selective coefficients applied among conspecific individuals for mating do not significantly alter heterospecific interactions during dispersal and local dynamics. This model pointed to similar results and highlighted the nonlinear response of speciation and community assembly across dispersal gradients (Fig. 3B).

Metacommunity perspective on speciation through fragmentation in landscapes

The most important contribution of neutral models has been to highlight that: (1) metacommunity spatial structure, and not just a physical barrier to gene flow (*e.g.* allopatric speciation), may lead to a gradual acquisition of reproductive isolation through spatial isolation (Fig. 3A) (Hoelzer *et al.* 2008; Desjardins-Proulx & Gravel 2012a,b), (2) speciation is a two-step process: (i) incipient species appear continually

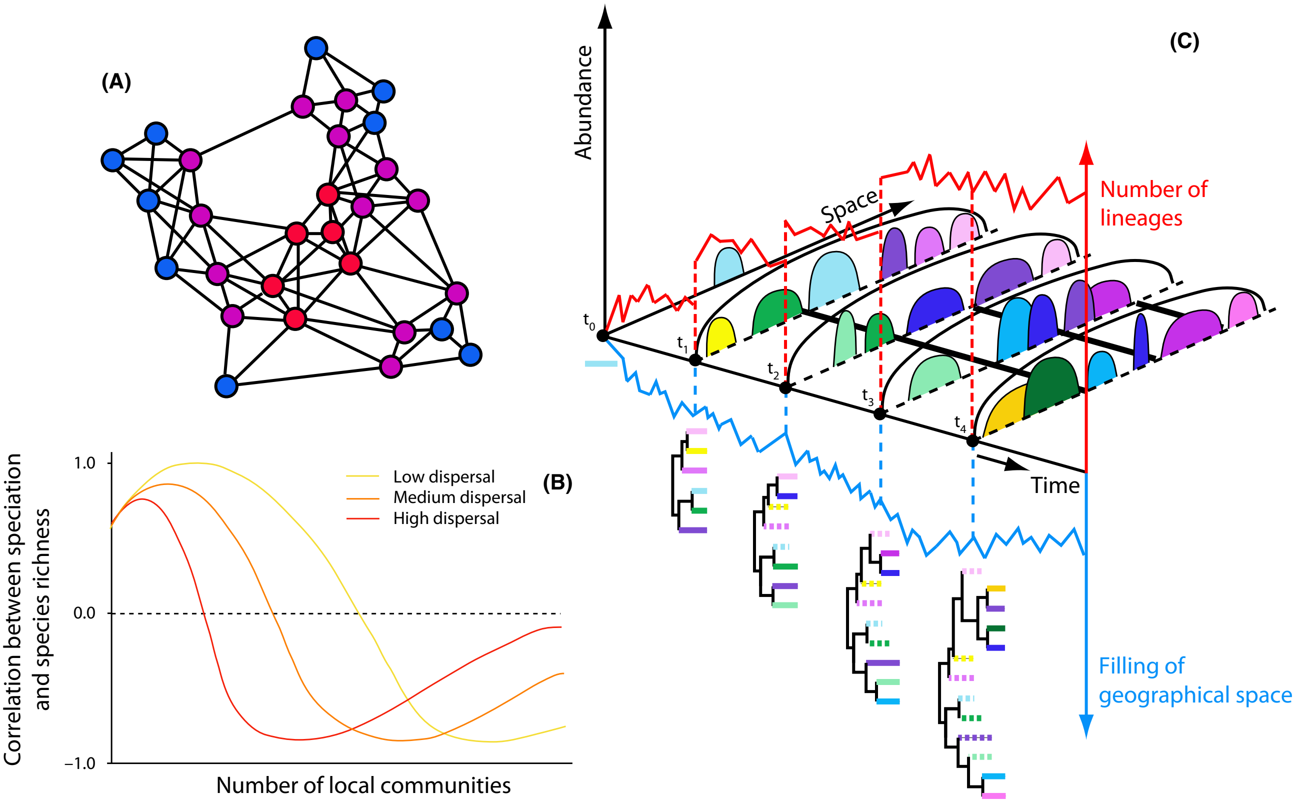

Figure 3 Patch connectivity, density, centrality and dynamics of speciation and community assembly in neutral metacommunities. (A) In a network of communities interconnected by dispersal, each node is characterised by its connectance (number of connections) locally and its degree of centrality (red, close to the centre; purple, intermediary; blue, border) regionally. (B) Variation in the correlation between speciation and species richness with increasing numbers of local communities and dispersal rates. At high dispersal or for many local communities, speciation occurs in peripheral nodes while species richness peaks near the centre. At low dispersal, speciation peaks in central patches where the probability of settlement of incipient species is highest. (C) Increasing diversity (red *y*-axis) by diversification through space (*z*-axis) and time (*x*-axis) following a neutral framework with the rise of barrier to dispersal during species diversification (bold lines) and stochastic variations in demographic parameters leading to varying species abundance (black *y*-axis).

(*i.e.* the real speciation rate following McPeek (2008)), (ii) an incipient species forms a novel 'good' species if it survives a transition period and establish in communities (*i.e.* the apparent speciation rate derived from empirical observations), a mechanism recently incorporated in the protracted speciation model by Rosindell and colleagues (Rosindell *et al.* 2010; Etienne & Rosindell 2012, 31–32 in Appendix S1).

Model II – Species-sorting and niche-mediated ecological speciation in environmentally heterogeneous landscapes

Species-sorting in communities

The theory of the niche has a long history in ecology and is considered as one of its central paradigms (Chase & Leibold 2003). While essentially considered a 'local' theory, it has been incorporated into the metacommunity framework either by assuming that species are sorted regionally according to their ecological niches (Leibold 1998) or are (partially) decoupled from this sorting through source sink or mass-effect dynamics (Mouquet & Loreau 2002; Ai *et al.* 2013) (Box. 2). In both cases, the number of coexisting species cannot exceed the number of limiting factors and niche differentiation takes place at the local (*i.e.* species sorting) or regional (*i.e.* source sink) scales (Figs 1 and 4A).

Niche-mediated ecological speciation

Most of the examples of ecological speciation described so far follow a two-step model: (i) adaptive divergence with limited gene flow (spatial fragmentation) fosters the settlement of pre-zygotic isolation mechanisms, (ii) post-zygotic isolation is possible through reinforcement upon secondary contact, *i.e.* selection against hybrids for which there is no niche (Schluter 2001; Turelli *et al.* 2001; Gavrilets 2004; Gavrilets & Vose 2006; Schluter 2009; Nosil 2012, 33–37 in Appendix S1). In sympatry, however, recombination breaks favourable allelic combinations and either higher selection coefficients or 'magic traits' determined by a limited set of genes should be involved (Turelli *et al.* 2001; Coyne & Orr 2004, 38–42 in Appendix S1). Generally, empirical studies on ecological speciation described an initial step of spatial isolation either through physical constraints or sorting of polymorphisms across patches with different ecological resources. In North American sticklebacks, for example adaptive shifts in body size and nuptial colouration across limnetic and benthic habitats induced assortative mating (43–44 in Appendix S1) followed by post-zygotic isolation involving differential growth rates of backcross hybrids whose rank order reverses between parental habitat (Schluter 2001). Similar pre-mating mechanisms of assortative mating have been shown to occur in *Drosophila* only after a few generations (review in Schluter 2001) and are generally accompanied by post-zygotic isolation through Bateson–Dobzhansky–Muller allelic incompatibilities (45 in Appendix S1). Several other examples of by-product ecological speciation have been discovered including Central American cichlids (46–47 in Appendix S1) or palms on oceanic islands (Gavrilets & Vose 2007, 48 in Appendix S1). We refer to Schluter (2009) for a compelling review.

Metacommunity perspective on niche-mediated ecological speciation

Populations occupying patches with spatially varying resources experience divergent selection that may trigger the settlement of reproductive isolation, depending on the relative importance of dispersal and gene flow, and descendant species are expected to exhibit narrower ecological requirements, so-called niche packing (McPeek 1996; Schluter 1998, 2001; McPeek 2008; Cornell 2013) (Fig. 1B2). Alternatively, evolutionary dynamics at play in communities during adaptation affect species coexistence through an intensified use of ecological resources by more specialised incipient species experiencing stronger competitive interactions (Vellend 2005; Vellend & Geber 2005; Urban 2006; Urban *et al.* 2008; Vellend 2010).

The rise of an evolutionary theory of the niche stressed that: (1) reproductive isolation may arise as a consequence of adaptation with gene flow in ecologically heterogeneous landscapes, (2) ecological dynamics at play in communities will influence speciation opportunities through competitive interactions for resources and (3) when evolutionary and ecological dynamics occur at the same temporal and spatial scales, their interactions can produce diversity patterns in communities that diverge from those expected when ecology and evolutionary dynamics are considered separately (Fig. 4B) (Wiens & Donoghue 2004; Urban 2006; Urban *et al.* 2008; Leibold *et al.* 2010; McInnes *et al.* 2011; Etienne & Haegeman 2012; Mouquet *et al.* 2012).

Model III – Patch dynamics, life history trade-off dynamics and community-mediated ecological speciation in environmentally homogeneous landscapes

Life history trade-offs and patch dynamics in communities

Competition for resources in environmentally heterogeneous landscapes has been considered in community ecological dynamics since the earliest development of the theory of the ecological niche (Mac Arthur & Levins 1967; Pianka 1976). Species using similar resources will compete and coexist only if some kind of adaptive shifts occur (Leibold 1998, 49–50 in Appendix S1). An alternative to the species-sorting niche-based mechanism of coexistence in metacommunities is based on the interplay between species interactions and trade-offs between life history traits enabling species coexistence on similar resources (*i.e.* patch-dynamics, Figs 1A and 5C, Box 3). In a set of species with different competitive and dispersal abilities, for instance, coexistence is possible if the traits related to both abilities trade-off appropriately (Hastings 1980; Hanski 1982; Gotelli 1991; Tilman 1994, 51 in Appendix S1).

Ecological speciation through biotic interactions and trade-offs in communities

This speciation model departs from the niche-based model of ecological speciation (Dieckmann & Doebeli 1999; Schluter 2001; Gavrilets 2004; Schluter 2009; Nosil 2012) by occurring in environmentally homogeneous landscapes and adaptive divergence is driven by the trade-off dynamics

Box 2 The niche paradigm

The theory of the niche accounts for species with certain ecological requirements such that the match between species niche and ecological resources in local patches determines species abundance (Chase & Leibold 2003; Leibold *et al.* 2004). In a heterogeneous landscape hosting varying resources among patches, community assembly is a deterministic function of species' matches to resources and dispersal (*i.e.* species-sorting) and speciation is a function of adaptation and gene flow among populations (*i.e.* ecological speciation). This paradigm holds for landscapes with environmental heterogeneity and no limitations to dispersal in which species compete to use resources according to their niche. From an evolutionary perspective, reproductive isolation results from adaptive shifts in traits defining ecological niches by natural selection *i.e.* ecological speciation (Schluter 1998, 2001, 2009) and community assembly is driven by the spatial scattering of ecological resources and species niches *i.e.* species-sorting (Leibold *et al.* 2004). In such systems, the correlation between species richness and speciation may be expected to peak at intermediary levels of both dispersal (Schmida & Ellner 1984; Mouquet & Loreau 2002; Urban *et al.* 2008; Ai *et al.* 2013) and spatial autocorrelation of resources across patches (Münkemüller *et al.* 2011). At high dispersal, maladapted species are maintained in local communities through source-sink dynamics (*i.e.* mass-effect) and speciation is inhibited by gene flow (Schluter 2001; Dieckmann *et al.* 2004; Urban 2006; Schluter 2009). At low dispersal, both speciation and species richness are favoured by limited gene flow and species-sorting dynamics (Gavrilets & Vose 2006).

The niche paradigm is based on the following initial assumptions:

(A1) Ecological heterogeneity (patches): patches are not ecologically equivalent and differ in the ecological resources available (landscape ecology).
(A2) Ecological heterogeneity (species): species *per capita* birth and death rates vary according to resources and each species has optimal rates for different resources (community ecology).
(A3) Ecological sorting (species): species abundances vary due to differences in resources among patches and a consequence of matching resources availability and species ecological optima (community ecology).
(A4) Mass-effect (species): source-sink dynamics allow species to persist in less favourable patches (community ecology).
(A5) Zero-sum dynamics (communities): resources are saturated at all times. This implies that resources made available by the death of an individual will be immediately used by a new individual and providing resources are constant, local communities are of constant size (community ecology).
(A6) Speciation is a deterministic population process driven by population adaptive shifts in response to environmental heterogeneity and gene flow (niche-mediated ecological speciation).

relating competitive abilities with alternative uses of space (*e.g.* competition/colonisation), predation and perturbation (*e.g.* competition/resistance to predation/perturbation) or reproductive tactics (*e.g.* competition/pollination; Fig. 1C1, C2), a model we refer to community-mediated ecological speciation.

Several empirical studies have described such adaptive mechanisms in natural populations. Langerhans and colleagues have shown, for instance, that the Bahamas mosquitofish (*Gambusia hubbsi*) populations have evolved adaptive changes in body size and caudal peduncle in the presence of its predator (*Gobiomorus dormitor*) associated with skewed female mate choice towards native males or males from similar predator regimes (52 in Appendix S1). Along the same line, the two sister species of monkey flowers *Mimulus lewisii* and *M. cardinalis* show different pollination syndromes (i.e. suites of flower traits that have evolved in response to natural selection imposed by different pollen vectors) as *M. lewisii* is pollinated by bumblebees while *M. cardinalis* is pollinated by hummingbirds. Schemske & Bradshaw (1999) have shown through crossing experiments that pollinators are attracted to artificial F2 hybrids in proportion to the mixture of the genes from the preferred parent (Schluter 2001, 2009). More recently, Yawata *et al.* (2014) demonstrated that competition–dispersal trade-offs fostered the ecological divergence of incipient species of marine bacteria.

Metacommunity perspective on community-mediated ecological speciation

The eco-evolutionary dynamics at play during community assembly ruled by life history trade-offs (*e.g.* competition/colonisation, competition/resistance to predation/perturbation) have been extensively studied through mathematical modelling in a metacommunity framework. Jansen & Mulder (1999) have shown, for example that diversity build-up may be easily explained by a trade-off between local growth and colonisation capacity and if mutation fuels new variants and sufficient competition occurs within a growth season, evolutionary community assembly through ecological speciation may be observed (Fig. 5A, B). Along the same lines, Bonsall *et al.* (2004) found that in communities of parasitoids where varying survival and attack rates are related to host density, trade-off dynamics may assemble evolutionary stable ecological guilds through ecological speciation. Gudelj *et al.* (2007) have also shown that in modelled microbial communities, different strains were able to coexist on the same source of energy as a consequence of trade-offs in ATP metabolic pathway between rates and yields of ATP production (Gudelj *et al.* 2007).

The development of an evolutionary patch-dynamics model in a metacommunity framework has highlighted that: (1) environmental heterogeneity is not a necessary condition for the

Box 3 The life history trade-off paradigm

This paradigm accounts for adaptive mechanisms in environmentally homogeneous landscapes based on competitive interactions and life history trade-off dynamics enabling species coexistence on similar resources in metacommunities (Hastings 1980; Hanski 1982; Gotelli 1991; Tilman 1994). In environmentally homogeneous landscapes, species will compete to access resources but species may coexist if life history traits related to competitive abilities and dynamics of colonisation or resistance to predation/perturbation are traded off appropriately (*i.e.* patch-dynamics). Competitive interactions and life history trade-offs may foster adaptive changes across trade-off space and lead to reproductive isolation (*i.e.* community-mediated ecological speciation). This paradigm holds for landscapes where competitive interactions limit species coexistence on similar resources and species co-occurrence is driven by life history trade-off dynamics among species. Following this paradigm, reproductive isolation results from adaptive shifts in the trade-off space as a consequence of competitive interactions fostering natural selection *i.e.* ecological speciation (Bonsall *et al.* 2004; Schluter 2009) and community assembly is driven by life history trade-off dynamics such as competition/colonisation or competition/resistance to predation/perturbation trade-offs *i.e.* patch-dynamics (Tilman 1994). In such systems, the correlation between speciation rates and species richness in metacommunities is determined by both the shape of the trade-off function and patch density (Jansen & Mulder 1999; Bonsall *et al.* 2004; Gudelj *et al.* 2007; Beardmore *et al.* 2011; Pillai & Guichard 2012). The shape of the trade-off function is determined by the strength of competition for space.

The life history trade-off paradigm is based on the following initial assumptions:

(A1) Ecological equivalence (patches): all patches are ecologically equivalent or ecological variations among patches do not impact species abundances (landscape ecology).
(A2) Ecological heterogeneity (species): species *per capita* birth and death rates are ruled by trade-off dynamics in life history traits preventing the optimisation of both resource use and dispersal (community ecology).
(A3) Competitive interactions: species abundances vary due to differences in optimised life history traits for resource use (competition) and dispersal (*e.g.* colonisation) or resistance to predation/perturbation (community ecology).
(A4) Mass-effect (species): source-sink dynamics allow species to persist in less favourable patches (community ecology).
(A5) Zero-sum dynamics (communities): resources are saturated at all times. This implies that resources made available by the death of an individual will be immediately used by a new individual and providing resources are constant, local communities are of constant size (community ecology).
(A6) Speciation is a deterministic population process driven by the existence of different local optima in competitive/dispersal abilities that trigger adaptive shifts among populations (community-mediated ecological speciation).

development of reproductive isolation through adaptive divergence as community composition may also constitute a driver of ecological speciation, (2) life history trade-offs dynamics may foster the settlement of eco-evolutionary dynamics in communities, analogous to those observed in a niche-based context and ruled by both local (*i.e.* adaptive changes in response to biotic interactions) and regional (*i.e.* dispersal) processes.

INTEGRATING SPECIATION THROUGH TIME IN METACOMMUNITIES: ECO-EVOLUTIONARY DYNAMICS AND DIVERSIFICATION

Metacommunity theory opened new perspectives on the impact of ecological dynamics on speciation opportunities (*i.e.* conditions of emergence of evolutionary community assembly, Fig. 2) and persistence of incipient species (*i.e.* transition period incipient species should survive). As diversity increases in communities, speciation is facing evolving ecological dynamics that in turn affect both speciation opportunities and species persistence, and impact speciation rates during community assembly (McPeek 1996, 2008; Cornell 2013, 53 in Appendix S1). During the last decade, there has been a major trend in macroevolutionary studies to explore the influence of ecological dynamics during community assembly on diversification through comparative methods (Cornell 2013; Morlon 2014). This approach led to a series of studies that focused on exploring the impact of filling niche space (*i.e.* species sorting and niche packing) and life history trade-offs (*i.e.* patch dynamic models and biotic interactions) on the pace of speciation during diversification. These studies intended to detect the signature of ecological dynamics in communities on several phylogenetic trees properties (*e.g.* phylogenetic tree shapes, phylogenetic community structure; Table 1). We will review in this section the phenomenology of this approach, from the first formal attempt to integrate evolutionary and ecological dynamics by the phylogenetic community structure approach to recent developments based on mechanistic approaches aiming at exploring the feedback of ecological dynamics on speciation through time.

Relating phylogenetic patterns with spatial dynamics

One of the first instances of integrating evolutionary dynamics into empirical community ecology is probably the community phylogenetic approach pioneered by Webb (Webb 2000; Webb *et al.* 2002; Mouquet *et al.* 2012, 54 in Appendix S1). Based on the assumption that closely related species frequently have similar traits and phylogenetic relationships mirror ecological divergence among species (55 in Appendix S1), Webb and colleagues proposed that community phylogenetic structure (*i.e.* local samples of the phylogenetic tree relating species from

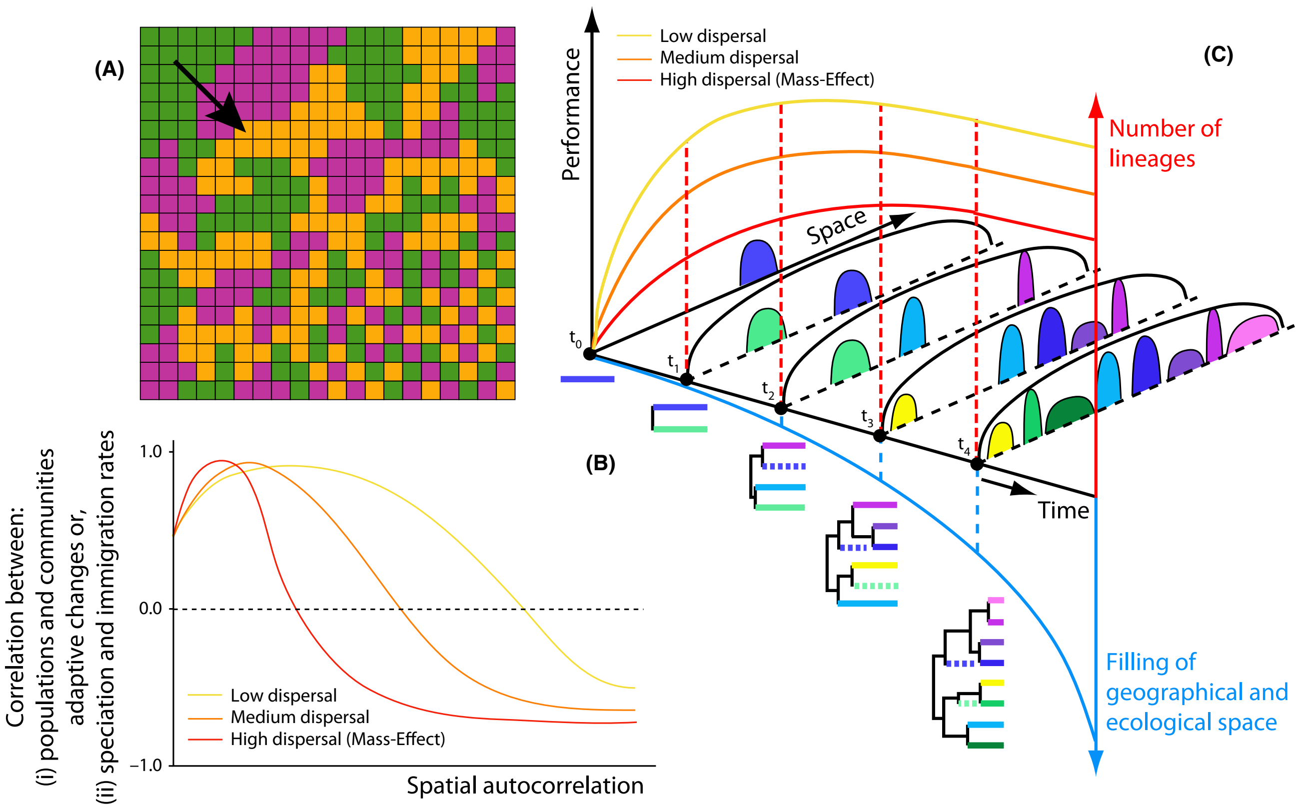

Figure 4 The spatial arrangement of ecological heterogeneity and dispersal determines the relative contribution of speciation and ecological sorting to the filling of resources and patches. (A) In a matrix of contiguous patches, the spatial sorting of resources can vary from spatial autocorrelation (top left) to random sorting (bottom right) following the arrow. (B) Response of the correlation between local adaptation (i.e. population adaptive changes) and colonisation of new patches (i.e. community adaptive changes) to varying spatial autocorrelation patterns (i.e. spatial heterogeneity in the distribution of resources) and dispersal rates. (C) Increasing diversity (red *y*-axis) by diversification through ecological space (*z*-axis) and time (*x*-axis) following niche-based dynamics determined by species' performance of resources use (black *y*-axis). Ecological specialists have narrow distributions in the ecological space (*z*-axis) but high performances (black *y*-axis). Ecological generalists have large distributions in the ecological space (*z*-axis) but low performances (black *y*-axis).

the regional pool) can be used to explore the dynamics of species sorting in communities and species turnover among communities based on several phylogenetic metrics and to trace back the processes underlying community assembly (Webb 2000, 56–60 in Appendix S1). Empirical studies provided different outcomes as both patterns of phylogenetic clustering or dispersion have been observed depending on the organisms and spatial scales involved (Table 1) (Emerson & Gillespie 2008; Vamosi *et al.* 2009) but identified key issues about the mechanisms of community assembly: (1) spatial scale dictates the relative contribution of historical and ecological factors resulting in varying patterns of community phylogenetic structure (Hubert *et al.* 2011, 61 in Appendix S1), (2) various combinations of spatial autocorrelation of ecological resources and mechanisms of coexistence can produce similar community phylogenetic patterns (Münkemüller *et al.* 2011), (3) modern coexistence theory tells us that both habitat filtering and competition can lead to phylogenetically clustered patterns, (4) ecological and evolutionary dynamics towards equilibrium between dispersal, speciation and extinction vary largely according to communities age (62 in Appendix S1).

Moreover, this approach highlighted that exploring the patterns of phylogenetic tree sampling in communities depends strongly on the speciation mechanisms (*i.e.* geographic or ecological speciation) and life history traits evolution associated (*i.e.* random, niche-related or trade-offs), two factors that affects the match of species traits to resources in communities (Leibold *et al.* 2010; Mouquet *et al.* 2012, 63 in Appendix S1). Speciation is determined by two main factors: (i) the landscape's physical (Fig. 3), environmental (Fig. 4) and ecological (Fig. 5) features that influence opportunities of speciation (Jansen & Mulder 1999; Schluter 2001; Bonsall *et al.* 2004; Hoelzer *et al.* 2008; McPeek 2008; Schluter 2009; Rosindell *et al.* 2010; Desjardins-Proulx & Gravel 2012a,b; Etienne & Rosindell 2012; Pillai & Guichard 2012), and (ii) the community background determining the persistence of new species in communities (Bonsall *et al.* 2004; Desjardins-Proulx & Gravel 2012a,b; Etienne & Rosindell 2012). Both mechanisms may be expected to influence the match of new species to their environment and communities, and impact ecological dynamics in communities.

Relating speciation with eco-evolutionary metacommunity dynamics

Understanding the influence of community ecology on speciation has been considered by evolutionary biologists trying to

Table 1 The three main paradigms of the metacommunity theory with their respective expected patterns regarding species coexistence, community assembly, phylogenetic community structure and diversification patterns including tree shape

Expected patterns	Hypotheses	References
(A) Physical heterogeneity of landscapes (neutral model (NM), geographic speciation)		
(P1) Species coexistence in local patches is a random process driven by stochastic variation in birth, death and dispersal rates in surrounding patches defining a network of local communities	Ecological equivalence (NM: A1, A2)	(Hubbell 2001; Chave *et al.* 2002; Alonso *et al.* 2006)
(P2) Species coexistence in the regional pool (metacommunity) is a random process driven by patch centrality and connectance in the metacommunity	Ecological drift (NM: A3)	(Hubbell 2001; Chave *et al.* 2002; Alonso *et al.* 2006; Economo & Keitt 2008, 2010; Desjardins-Proulx & Gravel 2012a,b)
(P3) Communities exhibit random to overdispersed patterns of phylogenetic relatedness depending on landscapes geometry: (a) for high patch density, speciation is not distributed randomly but occurs on peripheral patches leading to repeated pattern of speciation in space and enabling the settlement of phylogenetic community structure (overdispersed), (b) at low patch density, speciation is distributed at random and no phylogenetic community structure is expected	Ecological equivalence (NM: A1, A2) Ecological drift (NM: A3)	(Webb 2000; Webb *et al.* 2002; Etienne *et al.* 2007; Emerson & Gillespie 2008; Vamosi *et al.* 2009; Desjardins-Proulx & Gravel 2012a,b)
(P4) Diversity-dependent diversification: diversification is an area-dependent stochastic process driven by network constraints. During community assembly burst of speciation may be expected when an increasing number of patches are colonised depending on the size of the metacommunity leading to stochastic variations in diversification rates. As diversity increases, however, extinction rates increase because population sizes become smaller due to limited space	Zero-sum (NM: A4) Geographic speciation (NM: A5)	(Etienne *et al.* 2007; Rosindell *et al.* 2010; Hubert *et al.* 2011; Desjardins-Proulx & Gravel 2012a,b; Etienne & Rosindell 2012; Cornell 2013)
(P5) Phylogenetic trees balance is driven by species abundance evenness and speciation rates: (a) in large metacommunities with even species abundances and high speciation rates, phylogenetic trees tends to be balanced, (b) in small metacommunities with low speciation rates, species abundances are uneven and phylogenetic trees tend to be imbalanced	Geographic speciation (NM: A5)	(Hubbell 2001; Pigot *et al.* 2010b; Davies *et al.* 2011)
(B) Environmental heterogeneity of landscapes (species-sorting (SS), niche-mediated ecological speciation)		
(P1) Habitat filtering: Species coexistence in local patches (communities) is a stochastic process driven by the match of species ecological requirements with local patch resources	Ecological heterogeneity (SS: A1, A2)	(Cornwell *et al.* 2006; Kraft *et al.* 2007)
(P2) Niche partitioning: coexistence among species in metacommunities is enabled by adaptive shifts to alternative resources	Ecological sorting (SS: A3)	(Schoener 1974; Leibold 1998)
(P3) Communities exhibit average phylogenetic relatedness that vary from higher than expected at random to random patterns of phylogenetic relatedness depending on trait lability, spatial autocorrelation of resources and dispersal: (a) Phylogenetic clustering is expected when life history traits are conserved, resources are spatially autocorrelated and dispersal is low, (b) random to overdispersed patterns of phylogenetic structure are expected when traits are labile, resources randomly distributed or dispersal is high and support source-sink dynamics (mass-effect)	Ecological sorting (SS: A3) Ecological speciation (SS, ME: A6) Mass-effect (SS: A4)	(Webb 2000; Webb *et al.* 2002; Gavrilets & Vose 2006; Kraft *et al.* 2007; Vamosi *et al.* 2009; Münkemüller *et al.* 2011)
(P4) Diversity-dependent diversification: diversification slows down due to limited niche space or accelerate in empty ecological spaces	Zero-sum (SS: A5) Ecological speciation (SS: A6)	(McPeek 1996, 2008; Rabosky & Lovette 2008; Rabosky 2009; Pigot *et al.* 2010a; Kisel *et al.* 2011; Cornell 2013)
(P5) Phylogenetic tree balance is influenced by rates of adaptive changes and diversification, spatial autocorrelation of resources and dispersal: (a) departure from constant rates of diversification associated with key innovation or the colonisation of adaptive zones and/or spatial autocorrelation of resources and high dispersal will produce imbalanced trees as a consequence of uneven species abundance (b) random distribution of resources and low dispersal will favour the emergence of balanced to random phylogenetic trees	Ecological speciation (SS: A6)	(Schluter 2000a; Dieckmann *et al.* 2004; Phillimore & Price 2008; Pigot *et al.* 2010a; Davies *et al.* 2011; Etienne & Haegeman 2012)
(C) Heterogeneity of species life history traits (patch-dynamics (PD), community-mediated ecological speciation)		
(P1) Limiting similarity: coexistence in local patches (communities) is limited among closely related species as a consequence of adaptive shifts in life history trade-offs promoted by competitive interactions	Ecological heterogeneity (PD: A1, A2)	(Hutchinson 1959; Pianka 1976; Leibold 1998; Stubbs & Wilson 2004; Carlson *et al.* 2009)

(continued)

Table 1 (continued)

Expected patterns	Hypotheses	References
(P2) Life history trade-offs: species coexistence in the regional pool (metacommunity) is enabled by adverse effects between traits associated with competitive abilities and other traits (*e.g.* colonisation rate, resistance to predation/perturbation)	Competitive interactions (PD: A3)	(Levins & Culver 1971; Hastings 1980; Hanski 1982; Gotelli 1991; Yu & Wilson 2001)
(P3) Communities exhibit average phylogenetic relatedness lower than expected at random or random patterns depending on dispersal abilities and the existence of mass-effect dynamics	Ecological heterogeneity (PD: A1, A2) Competitive interactions (PD: A3) Mass-effect (PD: A4)	(Webb 2000; Webb *et al.* 2002; Münkemüller *et al.* 2011)
(P4) Diversity-dependent diversification: diversification slows down as space is filled and the life history trade-offs space is saturated	Zero-sum (PD: A5) Ecological speciation (PD: A6)	(Jansen & Mulder 1999; Bonsall *et al.* 2004; Gudelj *et al.* 2007; Beardmore *et al.* 2011; Cornell 2013)
(P5) Phylogenetic trees are imbalanced as a consequence of directional diversification in the life history traits space	Ecological speciation (PD: A6)	(Jansen & Mulder 1999; Bonsall *et al.* 2004; Gudelj *et al.* 2007; Beardmore *et al.* 2011)

explain the origin of the higher diversity in the Tropics since the 50s. Fischer (1960), Dobzhansky (1950) and Stebbins (1974), for instance, proposed that higher climatic stability in the tropics leads to lower extinction rates. Then, the higher diversity imposes stronger natural selection and species interactions that, instead of limiting niche space, promote speciation through character displacement (*i.e.* ecological speciation; 53, 64–65 in Appendix S1). Thus, regional diversity is expected to be unbounded and to be only limited by time and/or diversification rates (Cornell 2013, 53 in Appendix S1). Decreasing diversification rates through time have been frequently observed, however, and have been generally interpreted as the consequence of a feedback of local ecological dynamics on speciation (Ricklefs 1987; McPeek 1996, 66 in Appendix S1).

Are regional biotas bounded or unbounded?

The hypothesis of diversity-dependent diversification represents the first instance of a macroevolutionary model built upon the metacommunity framework that explicitly accounts for local dynamics on speciation (McPeek 1996, 2008; Phillimore & Price 2008; Cornell 2013). This hypothesis is derived from population growth models predicting that per capita birth and death rates converge in a limited environment as a population reaches its carrying capacity (*i.e.* the maximum biomass that can be supported by the resources in the environment) (Hutchinson 1959; Mac Arthur & Wilson 1967; Pianka 1976). It postulates that regional biotas have also carrying capacities in evolutionary time, a property based on the assumptions that communities are of finite size (*i.e.* the maximum biomass or individual that a community can support) and regional biotas are limited by the sum of the communities' carrying capacity (Cornell 2013). The metacommunity perspective, however, stresses the links between speciation and ecological dynamics through the influence of local (*i.e.* adaptation, competition) vs. regional (*i.e.* dispersal) dynamics on speciation (Jansen & Mulder 1999; Schluter 2001; Gudelj *et al.* 2007; McPeek 2008; Rosindell *et al.* 2010). Dispersal determines the relative contribution of evolutionary and ecological dynamics during community assembly if connectivity among patches is sufficiently high (Desjardins-Proulx & Gravel 2012a,b) or if the regional pool is rich enough to fuel communities with ecologically diversified immigrants (Jansen & Mulder 1999; Gudelj *et al.* 2007). During the early stages of community assembly, however, the low diversity in the regional pool may be expected to favour evolutionary dynamics (*i.e.* geographic and/or ecological speciation) and as regional diversity increases, ecological assembly likely offers fewer opportunities for speciation (Ricklefs 1987; McPeek 1996, 2008; Urban *et al.* 2008; Cornell 2013, 67–69 in Appendix S1).

Neutral and adaptive perspectives on bounded biotas

Two main mechanisms may be responsible for a feedback of ecological dynamics on speciation: (1) reproductive isolation may evolve more quickly during early stages of community assembly as a consequence of stronger disruptive selection due to a larger diversity of empty niches (*i.e.* species-sorting, Fig. 4C) or lower diversity of competitors (*i.e.* patch-dynamics, Fig. 5C); (2) speciation may be more difficult in saturated landscapes occupied by competing species because populations of newly diverged species may have difficulties to coexist with other residents (Schluter 1998, 2000a,b, 2001).

In a neutral context (Box. 1, Fig. 3, Table 1), species are ecologically equivalent and population sizes vary according to stochastic fluctuations in birth and death rates. Thus, in a metacommunity of finite size (*i.e.* the number of individuals is limited), extinction may be expected to increase with diversity because species population sizes become smaller due to limited space and become more prone to random walks to extinction (*i.e.* demographic stochasticity due to the community carrying capacity, Table 1). According to these dynamics, the probability of incipient species to persist in communities decreases with the number of species in the system and diversification rates will slow down as a consequence of increased extinction rates (Fig. 3). By contrast, adaptive models based on species-sorting (Box. 2, Fig. 4, Table 1) and life history trade-offs (Box. 3, Fig. 4, Table 1) predict that either the filling of niche space or the filling of trade-off gradients through evolutionary community assembly (Fig. 2) will lead to fewer speciation opportunities due to increased competitive interactions

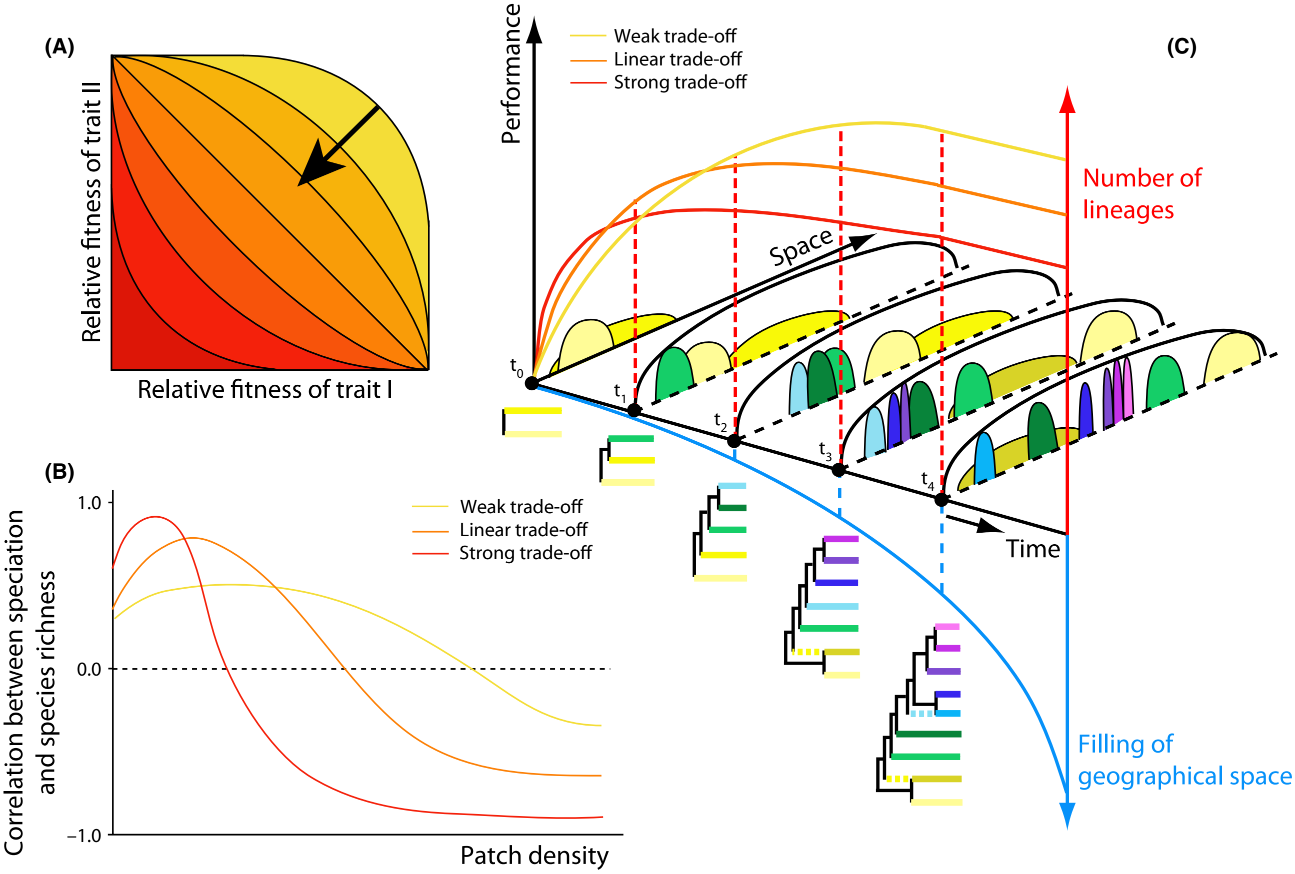

Figure 5 Trade-off functions, patch density and dynamics of speciation and community assembly through trade-off dynamics. (A) The increase in relative fitness through the optimisation of trait I will be mitigated through an adverse effect on trait II. The shape of the trade-off function defines the strength of the adverse effect ranging from weak (yellow) to strong (red). (B) Response of the correlation between speciation and species richness to patch density and shape of the trade-off function. At high patch density, source-sink dynamics may buffer local extinction and inhibit speciation by a higher coverage of the trade-off space. (C) Increasing diversity (red *y*-axis) by diversification through space (*z*-axis) and time (*x*-axis) following trade-off dynamics determined by species' performance of resources use (black *y*-axis). Following a competition/colonisation trade-off, good competitors have narrow distributions (*z*-axis) with high performances (black *y*-axis) but good colonizers have wide distributions (*z*-axis) with low performances (black *y*-axis).

(Table 1). Many attempts to test these hypotheses have been conducted using phylogenetic methods with diverse outcomes (McPeek 2008; Rabosky & Lovette 2008; Rabosky 2009; Paradis 2011; Rabosky *et al.* 2012, 70–71 in Appendix S1). Most of these studies focused on disentangling the relative contribution of early increases of speciation rates (*e.g.* empty ecological spaces offering greater opportunities of speciation) or late increases of extinction rates (*e.g.* higher demographic stochasticity due to smaller population sizes) to diversity-dependent diversification and several shortcomings may explain discrepancies among these studies: (1) disentangling speciation from extinction is a notoriously difficult task in phylogenetic reconstruction (Ricklefs 2007; Rabosky & Lovette 2008; Paradis 2011; Rabosky *et al.* 2012, 72 in Appendix S1), (2) modelling of ecological dynamics has been based on different models and assumptions (Gavrilets & Vose 2006; Phillimore & Price 2008; Gavrilets & Losos 2009), (3) only a few studies have incorporated spatially explicit models accounting for the antagonistic dynamics at regional and local scales (Gavrilets & Vose 2006; Gavrilets & Losos 2009; Desjardins-Proulx & Gravel 2012a,b; Pillai & Guichard 2012).

Integrating speciation mechanisms into the temporal study of diversification

The incorporation of speciation into metacommunity models offers a new perspective on the influence of the local and regional ecological dynamics on speciation in bounded biotas. As previously mentioned, Desjardins-Proulx & Gravel (2012a, b) showed that in neutral communities of large size, population size decreases during community assembly due to a finer partition of space among an increasing number of species (Table 1) and diversification rates become negatively correlated with species richness (Fig. 3B). Davies *et al.* (2011) explored the consequences of this random walk of species demography during diversity build-up on various phylogenetic trees properties, such as the balance and branching patterns of a tree, under varying conditions of diversity build-up in communities. The authors highlighted that neutral models make accurate predictions about the balance of phylogenetic trees but fail to predict branching patterns through time and account little for the tempo of species diversification in metacommunities (Table 1).

From a niche-based perspective (Fig. 4C, Table 1), Gavrilets & Vose (2006) showed by modelling evolutionary community assembly through ecological speciation on grids with varying ecological resources and hosting populations of varying size, that evolutionary community assembly can be achieved in a broad part of parameter space. The authors also showed that early bursts of speciation were observed in most of their simulations in agreement with the niche-based mechanism of diversity-dependent diversification (Gavrilets & Vose 2006). Hence, they identified through mathematical modelling potential mechanisms underpinning the feedback of local ecological dynamics on speciation and suggested by a large number of empirical studies, *e.g.* on Darwin finches (Schluter 2000b), Carribean *Anolis* lizard (Losos *et al.* 1998), Hawaiian spiders (Gillespie 2004) and Hawaiian sunflowers (73 in Appendix S1) among the most popular cases described so far (Gavrilets & Losos 2009, 74 in Appendix S1). Jansen & Mulder (1999), Bonsall *et al.* (2004), Gudelj *et al.* (2007) and Beardmore *et al.* (2011) reported similar patterns of evolutionary community assembly in evolving metacommunities following life history trade-offs models and observed two major trends in most of their simulations: (1) an earlier burst of diversification is observed when diversity is low and trade-off space is not filled, (2) phylogenetic trees tend to be imbalanced as a consequence of a gradual and unidirectional exploration of trade-off space (Fig. 5C, Table 1).

Integrating the study of speciation in a metacommunity framework paved the way for a fresh look at some of the oldest questions in evolutionary biology such as the condition of emergence of new species, or the evolutionary consequences of local dynamics in communities (Dobzhansky 1950; Fischer 1960; Stebbins 1974). By linking ecological and evolutionary dynamics across spatial scales through dispersal (*e.g.* Fig. 2), the metacommunity perspective has helped development of a unified framework that encompasses most of the complexity of the eco-evolutionary dynamics in communities and triggered a reappraisal of how speciation occurs and succeeds in building up diversity in communities.

SPECIATION IN METACOMMUNITIES: WHAT IS NEXT?

As detailed throughout this review, the metacommunity framework provides a common ground for integrating evolutionary and ecological perspectives and better appraising the complexity of speciation mechanisms. There is still a need for integration (Logue *et al.* 2011; McInnes *et al.* 2011; Mouquet *et al.* 2012), but we see here more opportunities for future research than limitations.

Considering species coexistence when studying speciation: beyond regional estimates of species range overlaps

Sister species are the most recent product of evolutionary dynamics in communities and their range overlaps potentially carry the imprint of local ecological dynamics (*i.e.* demographic stochasticity, adaptive shifts) on speciation (75–79 in Appendix S1). This sister-species approach was initially designed to disentangle the spatial context of speciation (*i.e.* allopatry vs. sympatry) from subsequent species range expansion at the regional scale but studies relying on this approach produced different results depending on the organisms and spatial scales involved (75–79 in Appendix S1). The approach was later improved by accounting for trait divergence into the study of range overlap dynamics among sister species and several of these studies detected a link between level of traits divergence and range overlaps (80–81 in Appendix S1). These studies, however, leaved unresolved the role of trait divergence during speciation either as a by-product of speciation (*e.g.* character displacement following secondary contact) or as the driver of speciation (*e.g.* magic traits). This limitation is due to the lack of integration of local dynamics inside communities (*e.g.* species-sorting, mass-effects) when considering range overlaps at the regional scale and as such, only partially accounting for the complexity of the ecological dynamics at play during speciation. Recent studies have stressed that considering co-occurrence data across transects or point observations may provide a broader understanding of the ecological dynamics inside communities on regional patterns of species range overlap and traits evolution (57, 82–83 in Appendix S1). Data on co-occurrence within communities are designed to appraise ecological dynamics influencing species coexistence and will lead the way for exploring speciation in a metacommunity framework. As emphasised throughout the present review, mechanisms driving species co-existence (*e.g.* competition for resources, life history trade-offs) impact both opportunities of speciation and persistence of incipient species. Analyses of range overlap between sister species should therefore move beyond regional estimates of species range overlap (*e.g.* percent of overlap between species range) and further include transects- or quadrats-based estimates of species occurrence and abundance to estimate co-occurrence and traits variability between sister species at the local scale.

Speciation in landscapes: accounting for metacommunities dynamics when studying speciation

Dispersal does not have a linear effect on ecological and evolutionary dynamics and their interactions may lead to different effects on speciation (Urban *et al.* 2008; Desjardins-Proulx & Gravel 2012b) (Fig. 2). From an ecological perspective, high dispersal rates enable the persistence of maladapted species in unsuitable patches (*i.e.* mass-effects) and mitigate extinctions due to demographic stochasticity. Sink populations will be maintained in patches independently of their ecological requirements but depending on immigration rates and proximity to source populations (Mouquet & Loreau 2002; Economo & Keitt 2008, 2010; Desjardins-Proulx & Gravel 2012a,b; Ai *et al.* 2013). This mass-effect may support coexistence of maladapted sink populations, whereas locally adapted source populations will persist through niche-based mechanisms (Urban 2006; Urban *et al.* 2008). From an evolutionary perspective, ecological speciation may produce incipient new species through niche-based dynamics in source populations. Source-sink dynamics, however, may foster their persistence in a nearly neutral model and extend incipient species' lifespan longer than expected and blur the impact of landscape ecological heterogeneity through mass-effects (Ai *et al.* 2013).

Gavrilets and Vose (2006) have demonstrated for instance, that diversity peaks during the early stages of adaptive radiations as a consequence of a higher number of transient species maintained by mass-effects and the latency of species diversification slowdown was proportional to island size. The lack of explicit incorporation of the effect of community size on species lifespan in the first neutral models may partially explain the lack of fit between empirical and modelling-based estimates of species lifespan in neutral models (Ricklefs 2003). Also, the distribution of resources in landscapes may influence source-sink dynamics by regulating the proximity of patches with varying resources (*i.e.* spatial autocorrelation of resources among patches) and as such, their potential connectivity (Münkemüller *et al.* 2011).

Overall, high dispersal rates lead to a scaling up of ecological dynamics from the local to the regional scale modifying the balance between ecological and evolutionary dynamics in such a way that communities may switch from one metacommunity coexistence mechanism to another depending on the scale of landscapes ecological heterogeneity and species dispersal abilities (Logue *et al.* 2011; Ai *et al.* 2013). This scaling up can be expected to affect speciation not only because communities are influenced by different ecological dynamics but also because ecological and evolutionary dynamics may act antagonistically. Recent studies have confirmed that species may be driven by different ecological dynamics in communities (*i.e.* species-sorting, mass-effect, trade-offs) depending on their life history traits and distribution (*e.g.* 84–85 in Appendix S1). Studying the ecology of speciation should move beyond the search of functional adaptive shifts related to resources use during evolutionary divergence and focus jointly on the impact of landscape (*e.g.* geometry, connectivity) and community features (*e.g.* demographic stochasticity, niche and life history trade-offs) on the phenomenology of species persistence. Recent developments in landscape genetics (86–89 in Appendix S1), for instance, may lead the way on how to integrate metacommunity dynamics when considering the eco-evolutionary dynamics in populations. Genotyping-based individual assignments (90–92 in Appendix S1), for instance, allow identifying an individual's source population and estimate the relative contribution of auto-recruitment in populations. This information may be further used to estimate the importance of mass-effect dynamics on sister-species coexistence in local communities and also identify the ecological dynamics at play in source populations (*i.e.* character displacement, trade-offs) and their impact on regional sister-species coexistence. Integrating this information across a large number of species in ecological communities may be expected to shed a new light on the influence of local ecological dynamics on the opportunities of speciation, the dynamics of persistence of incipient species and stress the conditions of emergence of evolutionary community assembly in empirical systems.

Species demography, eco-evolutionary equilibrium dynamics and timescales

Studies on insular radiations (Losos *et al.* 1998; Gillespie 2004; Emerson & Gillespie 2008) have shown that evolutionary community assembly may happen in short periods of time and thus provide useful insights into the interactions of eco-evolutionary dynamics at play during community assembly. Insular communities, however, represent particular cases of metacommunities where adaptive radiations, often thought to have an ecological basis, can happen when immigration rates are low (evolutionary community assembly in Fig. 2). From a broader perspective, Davies *et al.* (2011) have highlighted the link between species diversity and speciation through population demography and demonstrated that demographic stochasticity in metacommunities may account for the imbalance of phylogenetic trees (*i.e.* uneven distribution of diversity across clades). These authors and others (Melián *et al.* 2010; Davies *et al.* 2011) have pointed out that, if the probability of speciation is proportional to population size as expected under a neutral model, speciation is unevenly distributed across species according to their population size. As population sizes is likely to be influenced by the number of communities in a metacommunity (*i.e.* large metacommunities may sustain higher overall population sizes), metacommunity characteristics thus influence diversification by setting populations dynamics regionally. Linking diversification rates to demographic dynamics in evolving communities proved, however, to be a more difficult task (Melián *et al.* 2010; Davies *et al.* 2011).

Discrepancies between theoretical eco-evolutionary models and empirical inferences on diversification likely result from the time frame needed to achieve ecological equilibrium (*i.e.* stationary states where species richness and abundance are stable through time) and evolutionary equilibrium (*i.e.* stability in speciation and extinction rates leading to constancy in tree shape). First, tree imbalance and branching times are affected by different factors occurring at different timescales. Tree imbalance is influenced by stochastic fluctuations of population size affecting probabilities of speciation differentially across lineages while branching times result from the fluctuating balance between speciation and extinction. Second, ecological (*i.e.* dispersal vs. extinction) and evolutionary (*i.e.* speciation vs. extinction) equilibriums are reached along different timescales, a difference that may be expected to impacts eco-evolutionary dynamics at play in communities fluctuating towards equilibrium dynamics.

Non-equilibrium eco-evolutionary dynamics are expected, however, during the earliest stages of community assembly and both dynamics exercise reciprocal feedbacks that impact the dynamics towards equilibrium (Ricklefs & Bermingham 2001). Periods of spatial expansion into new patches and establishment of new communities, for example correspond to higher dispersal rates impacting evenness of species abundances according to their dispersal abilities and speciation rates among lineages (Emerson & Gillespie 2008; McPeek 2008). Non-equilibrium dynamics are important because landscapes are variable in nature as a consequence of recurrent perturbations ranging from random climatic events (*e.g.* cyclones, tsunamis, El Niño) to cyclic perturbations across evolutionary times (*e.g.* Pleistocene climatic oscillations) and exceptional events (*e.g.* major eustatic changes).

So far, the empirical study of eco-evolutionary metacommunity dynamics has relied mainly on historical inferences based on phylogenetic methods. This approach, however, is bridled by the limits inherent to any historical inference (*i.e.* old speciation and extinction events might not be traceable using molecular phylogenies). Comparative methods might not be the most appropriate approach to understand the feedback of demographic dynamics on speciation during community assembly, although, diversity-dependent diversification is fundamentally a phylogeny-derived property observed in many systems. Inferring species' past demographic trajectories during community assembly and relating it to fluctuating diversification rates through time seems a more suitable approach to explore the fluctuating impact of demography on speciation opportunities and incipient species persistence in empirical systems. Coalescent theory has enabled the development of analytical tools that are readily available for such inferences of populations past demographic trajectories (93–96 in Appendix S1). For instance, this approach should enable detecting a relationship between trends in past demographic trajectories and inferred diversification rates through comparative methods. The assembly of large genomic data for a large number of species has been circumvented by the next generation sequencing techniques enabling the implementation of community-wide demographic inferences. In a neutral context, for instance, earlier speciation events are expected to split sets of populations of larger sizes compared to the youngest speciation events and descendant species may be expected to exhibit both distinct molecular polymorphisms, as a consequence of varying species age and effective population size, and distinct demographic trajectories. In an adaptive context, niche packing may be expected to affect past demographic trajectories but this outcome is likely to depend on the distribution and relative abundance of the resources, two properties that affect the carrying capacity of resources and communities. Niche packing, for instance, may be expected to have led to a reduction in population size through time for the earliest species that formed in the communities as a consequence of increased competitive interactions and fine partitioning of resources use. Demographic dynamics, however, have been rarely taken into account in empirical studies of diversification (Phillimore & Price 2008; Davies *et al.* 2011) despite the emphasis on its importance by recent theoretical studies (Melián *et al.* 2010; Davies *et al.* 2011).

CONCLUDING REMARKS

The rise of metacommunity theory has led to a major improvement of our understanding of not only the mechanisms that enable the maintenance of diversity but perhaps more importantly, the mechanisms that increase diversity in communities (see for example Vellend 2010). Speciation and subsequent diversification are integrative processes that occur under given ecological conditions enabling not only the emergence of diversity but also its maintenance through time in communities. Ecological and evolutionary dynamics at play in communities are intricate and driven by nonlinear relationships at different spatial and temporal scales that further impact the mechanisms of species diversification. As such, the paradigms of the metacommunity theory and related speciation models have led to a more integrated appraisal of speciation either from an ecological perspective regarding its origin or its influence on the dynamics of community assembly. Recent integrative studies at the crossroads between macroevolution and metacommunity ecology provide opportunities for a comprehensive answer to some of the oldest questions in ecology and evolution such as on the origin of species, phenotypic divergence and species richness in landscapes. The combined development of new paradigms, mathematical models and integrative empirical studies already emphasises the benefit of using integrative eco-evolutionary frameworks to study the origin of diversity and we hope that our effort to synthesise the recent developments in this will make this approach more explicit and encourage new developments.

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