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CONTENT

The occurrence of two mactrid bivalves, *Mactra (Mactra) queenslandica* E.A. Smith and *Heterocardia gibbosula* Deshayes, in coastal water of Sidoarjo, East Java, Indonesia is reported here. The two species are examined and illustrated based on the local specimens collected. Previously, the distribution of *M. queenslandica* was reported only from northern – north-east Australia. This finding revealed that the distribution of this bivalve reaches Indonesian waters. Meanwhile, *H. gibbosula* is common in south-east Asian waters, however this is the first record for Indonesian waters. This result indicated that more mactrid bivalves could be discovered in Indonesian waters.

(Reni Ambarwati and Trijoko)

Scirpophaga incertulas is an economically important rice pest. A systematic investigation on the biological characteristics of ecological races linked to recent changes of agricultural practices and the environment has been conducted in order to assess genetic variation of *S. incertulas* in Indonesia. A 685bp segment of mitochondrial DNA, COII, was amplified from 42 yellow stem borer samples from five locations in Java (Madiun, Ngawi, Wonogiri, Tasikmalaya, and Indramayu). Six different haplotypes (YSB1, YSB2, YSB3, YSB4, YSB5 and YSB6) were identified in the sequenced yellow stem borer populations, with haplotype YSB2 being dominant.

(Hari Sutrisno)

Eight mite species of the family Macrochelidae (Acari: Mesostigmata) were collected from the body surface of dung beetles in Baluran National Park, East Java, Indonesia. Of these, one species, *Macrocheles subwallacei* sp. nov., is described as new to science. The female of *Macrocheles crispa* (Berlese, 1910) is redescribed and the male is described for the first time. The remaining six species are *Neopodocinum jaspersi* (Oudemans, 1900), *M. dispar* (Berlese, 1910), *M. hallidayi* Walter & Krantz, 1986, *M. entetiensis* Hartini & Takaku, 2005, *M. jabarensis* Hartini & Takaku, 2003 and *M. persimilis* Hartini, Dwibadra & Takaku, 2007.

(Sri Hartini, Dhian Dwibadra, Masahiro Ohara and Gen Takaku)

UDC: 574.9: 57.065

Rena Tri Hernawati

Exploring the dynamics during community assembly through community phylogenetics

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Species diversity through speciation and accumulate in ecological communities, a process known as community assembly. Relying on both evolutionary mechanisms acting at regional scale and ecological mechanisms acting at local scale, the process of community assembly results from intricate interactions among mechanisms at play across varying spatial and temporal scales. During the last decade, community assembly theory has been reconsidered in the light of evolutionary dynamics of species diversification and ecological dynamics have been formalised in an explicit spatial framework (*i.e.* metacommunity theory). The aims of the present review are: (1) to present the community assembly theory and the main paradigms that have been proposed, (2) to discuss how the metacommunity theory as defined an explicit spatial framework for community ecology, (3) to discuss the potential mechanisms at play during community assembly and their associated predictions, (4) to present new approaches to study community assembly based on phylogenetics approaches and discuss how they have been integrated in empirical studies.

(Rena Tri Hernawati, Daisy Wowor and Nicolas Hubert)

Key words: biogeography, community assembly, dispersal, phylogenetic community structure, speciation

UDC: 595.42 (594.81)

Sri Hartini

Macrochelid mites (Acari: Mesostigmata) from Kaimana,West Papua, Indonesia, and endemism of macrochelid mite fauna in New Guinea Island

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As a result of our investigation in Lengguru, Kaimana, West Papua, Indonesia, six species belonging to two genera of macrochelid mites (Acari: Mesostigmata: Macrochelidae) were collected from the body surface of dung beetles (Scarabaeidae). Of these, one is undescribed species *Macrocheles kaimanaensis* sp. nov. *Macrocheles hallidayi* Walter & Krantz, 1986 is newly recorded from Papua and West Papua (Indonesian parts of New Guinea Island). Males of *Holostaspella rosichoni* Hartini & Takaku, 2006 originally described from Papua were recorded for the first time. The other three species were *M. amaliae* Hartini, 2008, *M. dispar* (Berlese, 1910) and *M. waigeoensis* Hartini, 2008, which were previously collected from Raja Ampat, West Papua.

(Sri Hartini and Gen Takaku)

Key words: Indonesia, Kaimana, macrochelid mite, West Papua

EXPLORING THE DYNAMICS DURING COMMUNITY ASSEMBLY THROUGH COMMUNITY PHYLOGENETICS

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ABSTRACT

Species diversify through speciation and accumulate in ecological communities, a process known as community assembly. Relying on both evolutionary mechanisms acting at regional scale and ecological mechanisms acting at local scale, the process of community assembly results from intricate interactions among mechanisms at play across varying spatial and temporal scales. During the last decade, community assembly theory has been reconsidered in the light of evolutionary dynamics of species diversification and ecological dynamics have been formalised in an explicit spatial framework (*i.e.* metacommunity theory). The aims of the present review are: (1) to present the community assembly theory and the main paradigms that have been proposed, (2) to discuss how the metacommunity theory as defined an explicit spatial framework for community ecology, (3) to discuss the potential mechanisms at play during community assembly and their associated predictions, (4) to present new approaches to study community assembly based on phylogenetic approaches and discuss how they have been integrated in empirical studies.

Key words: biogeography, community assembly, dispersal, phylogenetic community structure, speciation

INTRODUCTION

Community assembly is the sum of the processes enabling and/or constraining the aggregation of species in an ecological community (Weiher & Keddy 1995). Community assembly happens along two main axes: (1) space (isolation and dispersal), (2) time (adaptation and speciation), both axes being variably involved during the colonisation process depending on the landscapes physical (*i.e.* connectivity) and ecological (*i.e.* resources) properties. The study of community assembly aims to explore how colonisation happens, and to estimate the relative contribution of processes such as immigration, habitat filtering, competitive interactions and speciation through time (Emerson & Gillespie 2008). At the regional scale (*i.e.* a collection of ecological community), dispersal among local communities occurs following variable rates through space and time while at the local scale (*i.e.* a collection of individual physically interacting in a community), competitive interactions and niche limits tend to limit the number of coexisting species (MacArthur & Wilson 1967). In

fact, community assembly is not expected to be constant through time as it results from the balance between dispersal, speciation and extinction, three antagonistic processes that are expected to fluctuate toward equilibrium dynamics through time (Gillespie 2004). Recently, phylogenetic data have been increasingly used in the study of ecological dynamics in communities and the study of the mechanisms driving species distribution (Webb 2002, Emerson & Gillespie 2008).

Recent advances in the study of community assembly will be discussed here. First, we will present the main paradigms of the community assembly theory that have been established in the literature. Second, we will present the metacommunity theory and spatial scales in the study of community ecology. Third, we will detail the ecological mechanisms during community assembly. Finally, we will present the new approaches integrating species abundance, phylogenetic relationships and null models in community ecology, and exemplify how these new approaches have been implemented in recent empirical studies.

Community assembly theory: focusing on mechanisms promoting species coexistence

Habitat filtering (or environmental filtering or phenotypic attraction) is the sorting of species within a community resulting from their tolerance to the abiotic environment (Weiher *et al*. 1998). Depending on the evolutionary trends in traits associated with species match to habitat (*i.e*. ecological resources), habitat filtering can lead to alternative patterns of community assembly (Table 1). If habitat filtering is driven by traits that are phylogenetically conserved, it will produce phylogenetically clustered communities. Conversely, habitat filtering driven by phylogenetically labile traits will tend to result in phylogenetically dispersed communities. Thus, depending on the evolution of traits, habitat filtering can lead to either phylogenetically clustered or dispersed communities (Webb 2002, Cavender-Bares *et al*. 2004, Kraft *et al*. 2007). Competitive interactions in ecological communities usually occur when species interact to access similar nutrients and their interactions may lead to mutual exclusion (*i.e*. limiting similarity). Competitive exclusion that limits the ecological similarity of co-occurring species should generate phylogenetic evenness (phylogenetic overdispersion) if the traits are phylogenetically conserved (Table 1). Alternatively, limiting similarity produces random or clustered patterns if the traits are convergent. On the other hand, neutral community assembly results from random dispersal and random species aggregation (Kraft *et al*. 2007). Thus, the phylogenetic structure of communities can be used to test for alternative models of community assembly based on habitat filtering, competitive

interaction or neutral assembly through the detection of departure of species phylogenetic relatedness from expected by chance, as conducted by Webb (2000) and Cavender-Bares *et al.* (2004) for instance.

Table 1. Patterns of community assembly and associated processes related to traits evolution (phylogenetically conserved or labile)

Assembly process	Traits evolution (phylogenetic pattern)	
	Conserved	**Convergent**
Habitat filtering (or environmental filtering or phenotypic attraction)*	Clustering of closely related species	Dispersion of closely related species
Competitive interaction (or limiting similarity or phenotypic repulsion)*	Dispersion of closely related species	Random or clustering of closely related species
Neutral assembly	Random dispersion	Random dispersion

*Some scientists (Webb 2002, Cavender-Bares *et al.* 2004, Kraft *et al.* 2007) use different terms to describe the same process.

Metacommunity theory: regional and local scales dynamics

A metacommunity (*i.e.* regional scale) is a set of local communities (*e.g.* local scale), fragmented in landscapes but linked among each other by dispersal of multiple interacting species (Fig. 1). A metacommunity has a spatial structure that consists of a large number of discrete patches (Wilson 1992) and community composition within a local patch may be affected by biotic interactions, resources and immigration (Fig. 1; Logue *et al.* 2011).
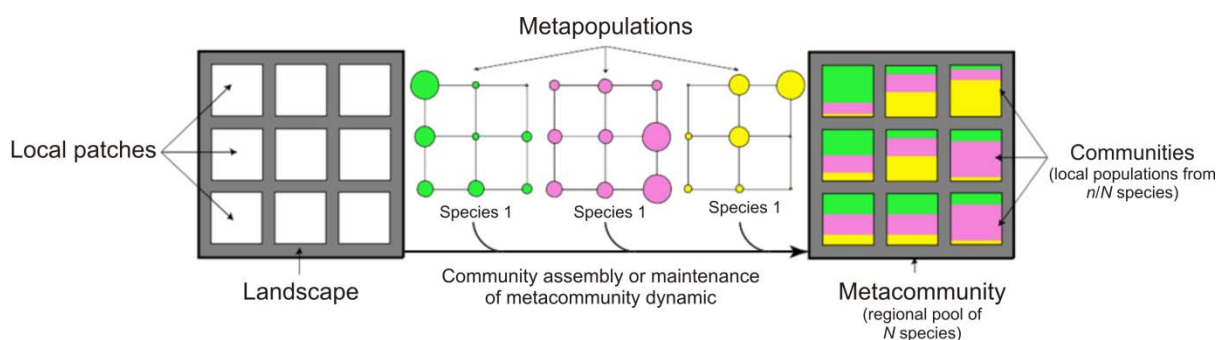
Figure 1. Schematic representation of the composition of a metacommunity. Local patches in landscapes are populated by *n* species among the *N* species available in the regional pool. Within each species, populations are more or less connected by dispersal (*i.e.* a metapopulation) and populations size vary among patches resulting in varying species abundances among patches.

From a numerical perspective, the theory of island biogeography has been the first theory to explicitly describe such metacommunity-like dynamic in a formal mathematical formulation (MacArthur & Wilson 1967). Given a mainland with *S* species exhibiting fluctuating population size and neighbouring islands at varying distances (isolation) from the

mainland with varied ecological conditions, each species have a probability to disperse (dispersal rate) from the mainland to the islands where they compete and adapt eventually until they get extinct and replaced by other species (Hanski 2010).This is the classical equilibrium theory of island biogeography (Fig. 2) firstly defined by MacArthur & Wilson (1967) and based on two assumptions. First, the rate of immigration of new species (*i.e.* those not yet on the island) decreases with increasing number of resident species (i.e. those already present). It reaches zero when all species in the source area (there are *S* of them) are on the island. Second, the rate of extinction of species increases monotonically as the number of species increases (the more species there are, the more to go extinct) (Schoener 2010). As a consequence, each island represents a subset of the mainland species pool resulting in local versus regional diversity relationships either characterised by linear relationships or asymptotic curves (Fig. 2B).
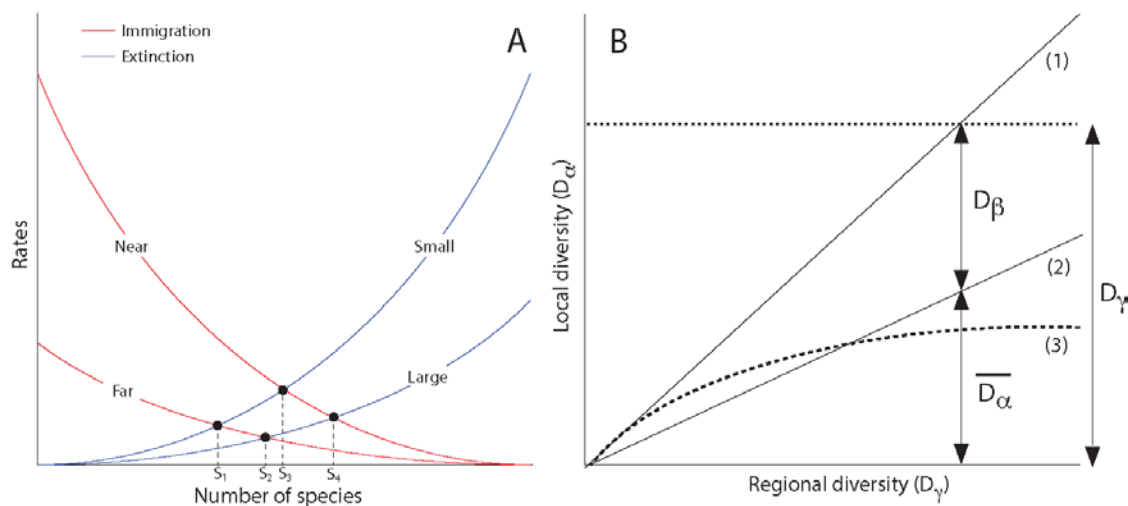
Figure 2. MacArthur and Wilson equilibrium theory of island biogeography and relationships between local and regional diversity. A, MacArthur and Wilson equilibrium curves describe the relationships among species richness, distance to the mainland, extinction and dispersal rates. S is the number of species at equilibrium when immigration equal with extinction. S_1, equilibrium for a small island (high extinction) far from the regional species pool (low immigration). S_2, equilibrium for a large island (low extinction) far from the regional species pool (low immigration). S_3, equilibrium for a small island (high extinction) near the regional species pool (high immigration). S_4, equilibrium for a large island (low extinction) near the regional species pool (high immigration). B, relationships between local (Dα) and regional diversity (Dγ): (1), the local diversity equals the regional diversity as a consequence of high dispersal and/or high connectivity; (2) linear relationship between local and regional diversity with a slope inferior to 1 as a consequence of limited dispersal among communities, a substantial amount of regional diversity is spatially distributed (Dβ); (3) local and regional diversity are related by an asymptotic curve due to the existence of a carrying capacity in ecological communities ceiling the maximum number of species able to coexist locally.

As demonstrated by the theory of island biogeography, community assembly relies on both ecological processes and biogeography. At the local scale, species that need similar resources will tend to be filtered into the same niche (*i.e.* phenotypic attraction). Competitive exclusion, however, is likely to happen among ecologically similar species and the strength

of this competition will depend directly of the ecological similarity among species. If species cannot adapt and modify their niche (*i.e.* character displacement), competitive exclusion will lead to the extinction of species in the community (Webb *et al.* 2002). Therefore, local scale is the scale of the factors limiting species coexistence and diversity in communities. By contrast, species disperse and colonise new places or islands and may occupy new habitats. During the time, they may adapt to the new ecological conditions and compete with other organisms. In doing so, they may complete speciation and generate endemic species (Wilson 1960). Thus, regional scale is the scale of the factors promoting species diversification. Both of local and regional scales show antagonistic mechanisms that interact and affect community assembly (*i.e.* local scale is limiting diversity and regional scale is promoting diversity).

Since both evolutionary and ecological mechanisms are involved during community assembly, a molecular phylogenetic approach has the potential to assess the relative roles of local and regional dynamics (Emerson & Gillespie 2008). Integrating ecology and historical biogeography may be expected to provide new insights into the dynamic of community assembly and to document large-scale patterns of species richness. Such integrative studies may be expected to shed light on several aspects of community assembly such as: (i) the ancestral ecological niche of a clade; (ii) the geographical starting point of dispersal; (iii) limitations to dispersal imposed by abiotic conditions and other species (*e.g.* niche conservatism and competition); (iv) opportunities for niche evolution that are afforded to species by their geographical location (*i.e.* species are unlikely to adapt to) and (v) the amount of time since the origin of the clade, during which niche evolution and dispersal could occur. Thus, integrative approaches may enhance our understanding of the interplay among processes such as dispersal, speciation, extinction and adaptation (Wiens & Donoghue 2004).

Ecological mechanisms during community assembly: dispersal, niche and species interactions

A fundamental question that ecologists frequently ask is how species niche influences biotic interactions and community assembly (Webb *et al.* 2006). Several theories have been produced but the theory based on the most limited set of assumptions is the neutral theory developed by Hubbell (2001) (Fig. 3). Hubbell's neutral theory is a stochastic theory based on a sampling model with dispersal-limitations (Alonso *et al.* 2006). Hubbell (2001) used the term neutrality for the assumption that interactions among species are assumed to be

equivalent on an individual basis. He also assumed that communities follow an ecological or neutral drift (species) as species abundances fluctuate and differ because of stochasticity in birth, death and dispersal *per se* (Table 2). Thus, ecological communities are called neutral when the differences between any pair of species in a community do not bring into a benefit for either of them (Alonso *et al*. 2006) and the fundamental factor maintaining the assembly of ecological communities is random dispersal (Hubbell 2001).
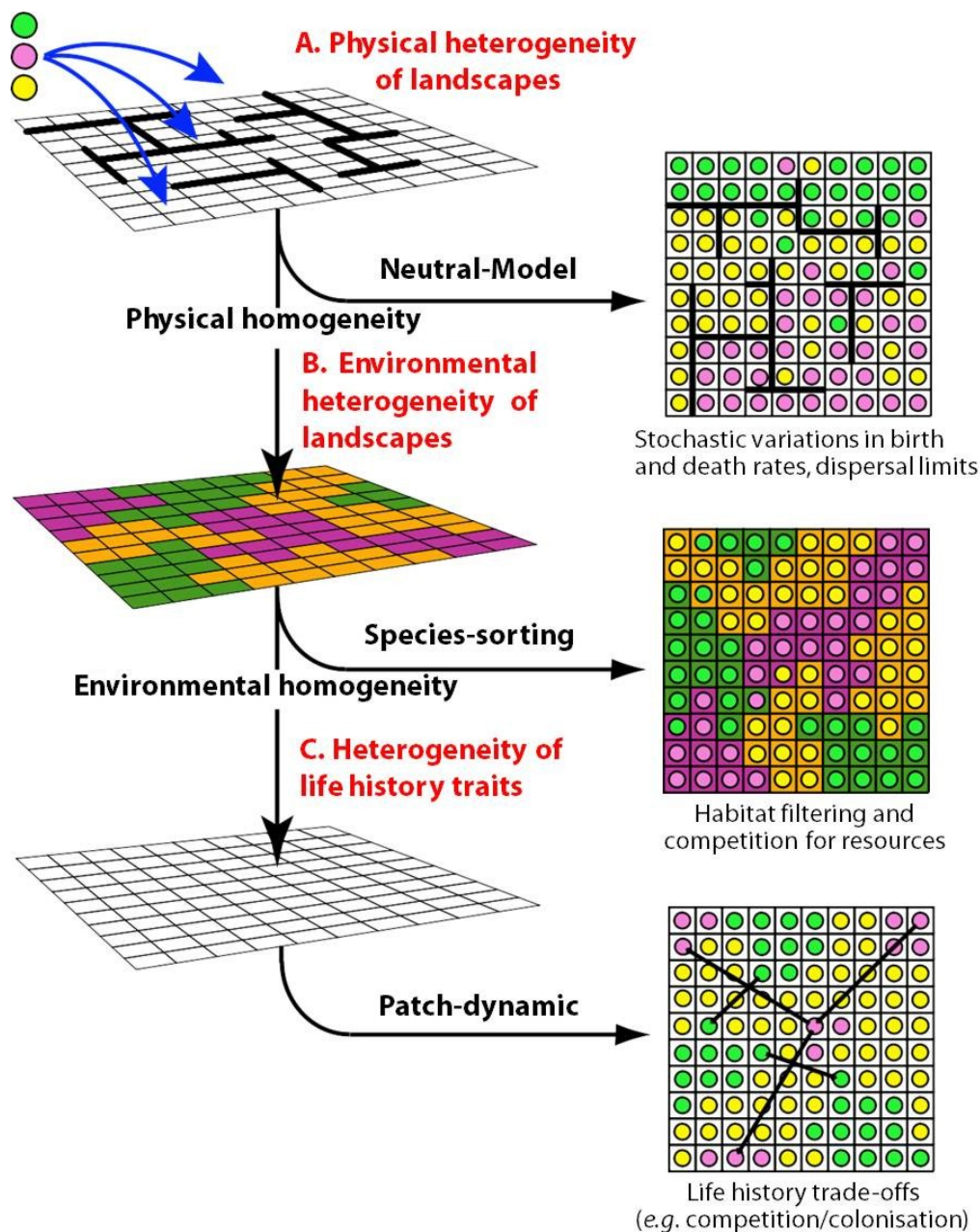
Figure 3. Three main paradigms of the metacommunity theory and associated properties of landscapes and species (modified from Hubert et al, *in press*). A, physical heterogeneity of landscapes constrains metacommunity dynamics and species abundances reflect stochastic fluctuations of demographic parameters (*i.e.* Neutral-Model). B, environmental heterogeneity of landscapes constrains metacommunity dynamics and species abundances reflect the match between species ecological requirements and resources (*i.e.* Species-sorting). C, heterogeneity of species life history traits constrains metacommunity dynamics and species abundances reflect competitive interactions and trade-offs dynamics (*i.e.* Patch-dynamic).

Alternatively, niche-based community assembly is driven by species traits (behavioural, physiological and morphological characters that define individual fitness) and the match of these traits to environmental resources (Leibold *et al*. 2004). Species-sorting is the metacommunity paradigm assuming that species coexistence is determined by the match between species ecological requirements (*i.e.* niche) and available resources in ecological communities (Table 2), and competitive interactions for resources. Species-sorting results in differences in population demography inside communities as a consequence of species interactions fostering ecological specialisation on ecological resources. This paradigm predicts that niche segregation has a greater impact on community assembly than other processes such as spatial dynamics (Leibold *et al*. 2004). Trait evolution is an important aspect of the match between species requirement and resources and traits between species can either converge or diverge. If traits in co-occurring species converge, they will evolve toward the same strategy to survive in given abiotic environments, hence exhibit the same ecological boundaries in a community (environmental filtering) and share similar phenotypic traits (Kraft *et al*. 2007, Kraft *et al*. 2008, Cavender-Bares *et al*. 2004). Habitat filtering will accumulate ecologically related species that have similar response to similar ecological conditions (Webb *et al*. 2002). By contrast, when species disperse, they may experience different ecological conditions that may trigger niche differentiation and traits divergence (Kraft *et al*. 2008).

Table 2. Assumptions of the main paradigms of the metacommunity theory (modified from Hubert *et al*, in press)

Paradigm	Assumption
Species sorting	- patches differ in the available ecological resources. - species birth and death rates vary according to resources - species abundances vary due to differences in resources among patches - source-sink dynamics allow species to persist in less favorable patches. - resources are saturated at all times (*i.e.* resources made available by the death of an individual).
Neutral models	- all patches are ecologically equivalent - interactions among species are assumed to be equivalent on an individual basis - species abundances fluctuate because of stochasticity in birth, death and dispersal - resources are saturated at all times.
Trade-offs	- all patches are ecologically equivalent - species birth and death rates are ruled by trade-off dynamics in life history traits preventing the optimisation of both resource use and dispersal. - species abundances vary due to differences in optimised life history traits for resource use (competition) and dispersal (*e.g.* colonisation) - source-sink dynamics allow species to persist in less favourable patches - resources are saturated at all times

Patterns of species diversity may be explained also by trade-offs within a homogeneous spatial framework (Table 2). Trade-offs, such as competition-colonisation trade-off, may account for alternative mechanisms of species coexistence by assuming that if species traits are traded-off appropriately, species can persist in ecological communities by developing alternative strategies (Chesson 2000, Kneitel & Chase 2004). For example, a trade-off between seed size and seed number (Levine & Rees 2002) will impact competitive ability that is increased by the production of fewer, larger seeds, whereas colonisation ability is enhanced by the production of many small seeds (Kneitel & Chase 2004).

Phylogenetic Community Structure: a new approach to study community assembly

Null model in community ecology: the neutral theory

Null models are used to test departures in empirical observations from the patterns expected by chance and many ecologists have been using null models in community ecology since the study of genus/species ratio (MacArthur & Wilson 1967). In small islands, for instance, the ratio of the number of species per genus is generally lower than in the mainland, as a result of the increased impact of competitive interactions among congeneric species in small areas with limited carrying capacities (MacArthur & Wilson 1967). While MacArthur & Wilson (1967) proposed a null model based on equilibrium between speciation and extinction through time, this equilibrium theory does not account for the complexity of ecological communities in species rich ecosystems. The neutral theory, later developed by Hubbell (2001) based on MacArthur and Wilson theory, is an equilibrium theory that improved our understanding of the dynamic at play in ecological communities by offering a null model that integrate more of the complexity in ecological communities than MacArthur and Wilson model. The neutral theory led to the development of models able to predict species richness and abundance, and later phylogenetic community structure and phylogenetic tree shape under a simple null model assuming random dispersal and species aggregation (Hubbell 2001).

Null models have been widely used in empirical studies because they can be applied for testing the departure of empirical observations from random patterns. In previous studies, such as Fisher's log series (Fisher *et al*. 1943), Preston's log normal (Preston 1948) and MacArthur's broken-stick hypothesis (MacArthur 1960), the authors have developed functions to match abundance distribution curves in empirical observations. Most of these theories, however, are based on statistical distributions that hardly apply to empirical studies (*i.e*. small sample sizes) and do not account for the relationship between phylogeny and

relative abundance (Hubbell 2001, Webb 2002). Null models, for instance (Hardy & Senterre 2007), can be used to compare observed phylogenetic distances among species to the distribution of phylogenetic distances expected by chance (*e.g.* random community assembly) and resulting from a testable null hypothesis (*i.e.* no phylogenetic signal) (Fig. 4). Partial randomisation of the tip of the phylogenetic tree based on species age thresholds may be used to investigate the significance of phylogenetic community structure according to the phylogenetic depths of the species sampled in the community. Hence, randomisation procedures can be applied to detect departure from random estimates (Hardy & Senterre 2007).
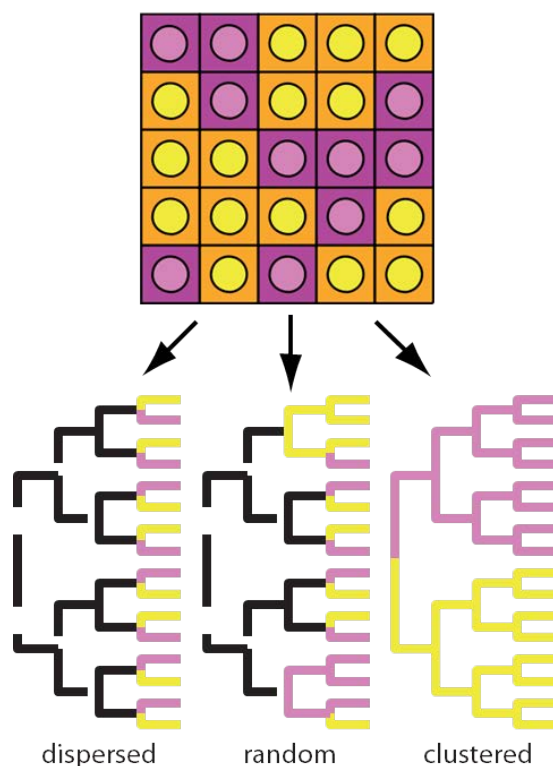
Figure 4. Patterns of phylogenetic community structure expected according to varying levels of phylogenetic relatedness. The dispersed and clustered patterns are a consequence of respectively lower or higher phylogenetic relatedness in communities compared to a random pattern. The 5 x 5 cells grid represents a metacommunity with each cell representing a patch and each patch supporting a population. The colour of the patch defines it ecological niche while the colour of the circle represents the niche preferred by the majority of the individuals (*i.e.* the strategy giving the highest probability of survival). In all trees, each tip represents a species, branch colors represent the niche preference and dotted branches correspond to ambiguous ancestral characters states following the parsimony criterion.

Phylogenetic diversity indices

Since the first indices of diversity developed by Shannon (1948) and Simpson (1949), new indices that incorporate evolutionary relationships among species have been proposed (Webb *et al.* 2002, Hardy & Senterre 2007, Cadotte *et al.* 2010). Faith (1992), for instance, proposed an index of Phylogenetic Diversity (Faith's index) that corresponds to the sum of all

the phylogenetic branches connecting species within a sample (*e.g.* a community). This index, however, does not incorporate information on the relative abundance of taxa within communities. Webb *et al.* (2002) have been among the pioneers of the exploration of the link between species phylogenetic relationships, traits evolution and ecological dynamics during community assembly and proposed several indices such as the Mean Phylogenetic Distance (MPD) and the Mean Nearest Taxon Distance (MNTD) that can be computed for any set of species (*e.g.* a transect, a plot). MPD corresponds to the average phylogenetic distance among species and MNTD corresponds to the average phylogenetic distance to the closest phylogenetic neighbor. For any set of species with known phylogenetic relationships, both indices can be computed and compared to the estimates obtained from randomly generated samples (random re-sampling of species).

Webb *et al.* (2002) further developed indices that account for sampling size effects (*i.e.* uneven distribution of sampling size), the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) that are derived from the difference between empirical estimates and estimates obtained based on replicated permutations, standardized by the standard deviation of index in replicates (Webb *et al.* 2002):

$$NRI \ = -1 \times \frac{MPD_{observed} - MPD_{null}}{sd(MPD_{null})}$$

$$NTI \ = -1 \times \frac{MNTD_{observed} - MNTD_{random}}{sd(MNTD_{random})}$$

Positive NRI and NTI show that species occurring together are more closely related than expected by chance due to phylogenetic clustering of co-occurring species. By contrast, negative NRI and NTI show that species co-occurring are less phylogenetically related than expected by chance as a consequence of phylogenetic overdispersion (Cavender-Bares 2006, Kembel & Hubbell 2006, Hardy & Senterre 2007).

Phylogenetic community structure indices

More recently, Hardy & Senterre (2007) proposed indices to test community phylogenetic structure among communities that account concomitantly for species abundances and phylogenetic relationships. They use the initial statistical formulation of Simpson diversity index that quantifies and partitions additively species richness into alpha (α) and beta (β) components with β-diversity representing the compositional variation among communities from site-to-site, linking local (α-diversity) and regional (γ-diversity)

(Fig. 2; Chase *et al.* 2011). They modify those formulations as follow: D^{I} (Simpson diversity index) and D^{P} (an index of phylogenetic diversity) based on index of species identity I_{ST} and species differences P_{ST} (including the number of individuals per species per site or abundance data values), respectively.

$$D^{\mathrm{I}} = \Sigma D_c^{\mathrm{I}}$$

Where D_c^{I} is the probability that two individuals belong to distinct species whose divergence time is included in class c (classes must be non-overlapping and cover the full range of divergence times between species).

$$D^{\mathrm{P}} = \Sigma_c \delta_c D_c^{\mathrm{I}}$$

Where δ_c is the average divergence time corresponding to class c.

Those equations can be extended to create D_T (the total (γ) diversity), D_k (the diversity within site k), and D_S (the expectation of D_k over all sites). Incorporating of all formulations to species identity I_{ST} and species differences P_{ST} as follows:

$$\hat{I}_{ST} = \frac{\widehat{D}_{\mathrm{T}}^{\mathrm{I}} - \widehat{D}_{\mathrm{S}}^{\mathrm{I}}}{\widehat{D}_{\mathrm{T}}^{\mathrm{I}}}$$

$$\hat{P}_{ST} = \frac{\widehat{D}_{\mathrm{T}}^{P} - \widehat{D}_{\mathrm{S}}^{\mathrm{P}}}{\widehat{D}_{\mathrm{T}}^{\mathrm{P}}}$$

Furthermore, Hardy & Senterre (2007) new approach is nested in the above statistical framework to test phylogenetic community structure. The mean phylogenetic distance (Π_{ST}) between species found in different sites compared with species found within sites, and requires only incidence data (presence/absence of each species in each site) are expressed by:

$$\widehat{\Pi}_{ST} = \frac{\widehat{\Delta}_{\mathrm{T}}^{\mathrm{P}} - \widehat{\Delta}_{\mathrm{S}}^{\mathrm{P}}}{\widehat{\Delta}_{\mathrm{T}}^{\mathrm{P}}}$$

There are two analogies D^{P} by analogy with Δ^{P} and P_{ST} by analogy with Π_{ST}. The expectation is $\Pi_{\mathrm{ST}} = 0$ when there is no community phylogenetic structure and $\Pi_{\mathrm{ST}} > 0$ ($\Pi_{\mathrm{ST}} < 0$) under phylogenetic clustering (overdispersion).

Empirical studies of community phylogenetic structure

Terrestrial organisms

The phylogenetic community structure has been already explored in many terrestrial communities, especially in plants (Vamosi *et al.* 2009, Emerson & Gillespie 2008). Most of them relied on plots sampling to estimate species abundances in communities. For instance, Webb *et al.* (2000) sampled 28 plots of Borneo rain forest (40 ×40 m^2) where they detected

324 species. The authors used the NRI metric to explore the phylogenetic structure of tree communities and observed that species were more phylogenetically related than expected by chance, a result that was insensitive to various modifications of the basic methodology (Webb *et al.* 2000). Borneo rain forests have ecologically and phylogenetically more similar tree species co-occuring within plots than caused by chance as a consequence of variation in habitat among plots (Webb 2000).

Hardy & Senterre (2007) studied plant phylogenetic community structure in 28 plots of 25×25 km^2 within the Monte Alén National Park in Equatorial Guinea and measured several ecological characteristics within each plots (*i.e.* altitude, stand dynamic (intensity of perturbation assessed from the frequency of windfall gaps; three ordinal classes), hygrometry, soil hydromorphy, soil depth, presence of rocks in the soil and presence of an impenetrable gravel layer in the soil). The authors explored the phylogenetic community structure through partial randomisation within families and found no evidence of phylogenetic structure within families. By contrast, partial randomisation using age thresholds showed that some phylogenetic clustering was related to some deep phylogenetic splits. In addition, the authors evidenced significant positive correlations between the plots ecological distance and phylogenetic structure as ecological heterogeneity explained 17% and 29% of the variance of Π_{ST} and P_{ST} respectively.

Studies on phylogenetic community structure in animal communities evidenced more contrasted patterns, however, partially because these studies focused on animals with different dispersal abilities and varying spatial scales. Phylogenetic community structure in songbirds (wood-warbler) was investigated by using Breeding Bird Survey (BBS) transects (Lovette & Hochachka 2006). The authors evidenced that species with largely overlapping range distribution at the regional scale were scarcely co-occurring locally and the degree of local co-occurrence was inversely related to phylogenetic relatedness (*i.e.* closely related species almost never co-occur locally). Behavioural differentiation (forage in similar vs. mixed vegetation strata) had a significant role to habitat use and to reduce the interspecific competition (limiting similarity) as a consequence of habitat specialisation. Hence, more distantly related species will co-exist locally more often than expected by chance.

Aquatic organisms

Empirical studies in aquatic organisms are few but provide insightful information about the dynamic at play during community assembly of aquatic organisms. For vertebrates,

Hubert *et al.* (2011) investigated community assembly in coral reef fishes at both inner reefs and outer slopes sites in Madagascar, Reunion, and French Polynesia, in sampling plots of 20 x 20 m^2. The authors inferred the phylogenetic relationships of the 157 species sampled through the analyses of mitochondrial DNA sequences. At local scale, the authors observed positive Π_{ST} values for each of the islands but Π_{ST} values were not significantly different from expected by chance, a pattern consistent with a neutral model of species coexistence. At the regional scale, Π_{ST} values estimated for subsamples of species across divergence intervals of 5 Ma indicated that the most recently derived species were following a pattern of phylogenetic overdispersion as a result of allopatric speciation in recent time. They concluded that community assembly occurs through random dispersal at the local scale in coral reef fishes as a consequence of the unpredictable nature of coral reefs but regional dynamics are likely to result from allopatric speciation.

Integrating ecological data and morphological measurements (body size) also produced insightful results about community assembly for invertebrates (Vamosi & Vamosi 2006, Hultgren & Duffy 2012). Vamosi & Vamosi (2006) explored the community structure of diving beetle assemblages of Alberta and the relationship between body size, rarity traits and phylogenetic community structure. The total length of dytiscid species ranged from 2.91 mm to 32.90 mm and dytiscid occurrences ranged from rare or infrequent, such as *Oreodytes congruus* (being found in only one lake), to widespread, such as *Laccophilus biguttatus* (found in 15 lakes). The lake-dwelling dytiscids exhibit conserved traits (body size and rarity) but the authors evidenced no relationship between rarity and community species richness or between TL and community species richness. Both NRI and NTI values, however, were not significantly different from those obtained by permutation but higher variance in both NRI and NTI tended to be found in lakes with lower species richness (*i.e.* small community with fewer species).

Morphological measurements may also help characterise species niche and bring additional information about community assembly. Hultgren & Duffy (2012), for instance, explored the structure of the communities of eusocial sponge-dwelling shrimp (*Synalpheus*) by using different traits such as carapace length (CL) and their specific sponge host (canal size). In parallel, they used molecular data (COI, 16S and nuclear gene elongation factor 2 EF2) to estimate species phylogenetic relationships. The authors evidenced that sponge-dwelling shrimps (*Synalpheus*) assemblages are influenced by habitat-size as there was a relationship between body size heterogeneity and ecological heterogeneity since greater

patches with diversified niches are associated with higher size heterogeneity. The authors also evidenced that species interact through competitive exclusion mediated by social system and territoriality since *Synalpheus* shrimp were less phylogenetically related and less similar in traits inside than among communities. This result suggests that eusociality may be able to drive competitive interactions and competitive exclusion (Hultgren & Duffy 2012, Webb *et al*. 2002).

CONCLUSIONS

Community composition is predicted to fluctuate through time. At local scale, co-occurring species may interact and compete to access resources. At regional scale, species distribution ranges are fragmented and experience diverse biotic and abiotic conditions eventually leading to speciation. As metacommunity dynamics are driven by both local and regional dynamics, these dynamic are not expected to be constant through time since species abundances and community composition fluctuates through time. The metacommunity theory, however, helps to investigate the factors affecting the ecology and evolution during community assembly by setting an explicit spatial framework.

The theory of island biogeography by MacArthur & Wilson (1967) was the initial attempt to develop formal mathematical models to describe metacommunity dynamics. This initial theory has been further developed by Hubbell (2001) through the rise of the neutral theory of biodiversity that open new perspectives in the study of community assembly by providing an explicit null model for exploring community dynamics. As such, the neutral theory was an improvement toward the detection of alternative mechanisms including ecological niches and competitive interactions. The development of models integrating species abundances and phylogenetic relatedness paved the way for integrative approaches in community ecology and the joint exploration of ecological and evolutionary dynamics during community assembly.

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