

What do spatial and evolutionary biodiversity patterns tell about underlying processes?

An Introductory Essay by Leonel Herrera Alsina

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Introduction

Ecological communities or species assemblages, albeit of plants, animals or microbes, display an enormous diversity. Yet, very distant communities may also be rather similar. For instance, lizard communities in California and Australia show a striking similarity in ecomorphological structure and habitat preference (Melville et al. 2006). This convergence of communities despite the separation by a long distance suggests that both assemblages are governed by the same general mechanisms. These mechanisms, which include habitat filtering and ecological competition, determine biodiversity patterns such as community composition, species abundances and spatial distributions. However, to find what mechanisms are responsible is not a straightforward task, particularly because one must consider spatial and temporal dynamics at large scales (Ricklefs 1987). Phylogenetic patterns are generally believed to inform us about their relative importance (Webb et al. 2002) although recently doubt has been cast on how much we can infer from these patterns (Mayfield and Levine 2010, HilleRisLambers et al. 2011, Gerhold et al. 2015). Nevertheless, ecological competition between phylogenetically or ecologically similar species plays a crucial role in determining which species can enter a species assemblage (Diamond 1975). Empirical evidence of this comes from biological invasion studies: the inclusion of a potential invader species to a community is a function of phylogenetic similarity (i.e., as a proxy of ecological similarity) between the invader and the native community members (Jiang et al. 2010) and thus also depends on the order in which species arrive in the community. A recent study on geographic ranges of sister species pairs confirms this: as their phylogenetic separation increases, they are more likely to have overlapping ranges (Pigot and Tobias 2013). This result inspired me for the proposed project in which I aim to study how community assembly processes can affect geographic ranges, and how information on these processes can be inferred from data on geographic ranges.

One might describe richness as the number of species' geographic ranges that overlap at a given site. Analyzing range size and diversity patterns may thus

provide useful insights. For example, for the North American mammals Arita et al. (2008) showed that range-restricted taxa occur in high diversity areas which often are located in tropical zones. Most species are range-sized restricted (e.g. the Long-Whiskered Owlet (*Xenoglaux loweryi*) with a range size of 177 km²) while few are widespread (e.g. Mountain Pygmy Owl (*Glaucidium gnoma*) with a range size of 600 000 km²), producing a right-skewed range size frequency distributions (Orme et al. 2006). The question then arises whether this pattern, along with other patterns, contains information about assembly processes.

Range size can be considered as a species' trait (or character state). Although range size is not an intrinsic property of organisms, it is an emergent attribute of species and – like other emergent attributes, such as abundance (Rosindell et al. 2015) – it evolves through evolutionary time (Jablonski 1987). According to the fossil record, stages of expansion and contraction seem to be the way the range size evolves (Liow and Stenseth 2007, Pigot et al. 2012). The functional traits of individuals can influence both speciation and extinction rates which in turn drive macroevolutionary assembly of communities. For example, skull configuration is related with high diversification in phyllostomids bats (Dumont et al. 2012). Dioecy in angiosperms seems to be a condition which hinders speciation or perhaps increases extinction probability leading to clades of lower diversity compared to their sister clades with different breeding systems (Heilbut 2000). Likewise, range size can influence speciation and extinction rates. For instance, a geographically restricted species is more likely to suffer extinction. Likewise, within the geographic range of a widespread species, vicariance events are more prone to happen increasing the probability of speciation. However, the way range size is inherited during speciation processes is different from individual-level traits. For example, in the case of body size, each of the daughter species arising from a speciation event will tend to inherit a value for this trait which is similar to the ancestor. In contrast, when the geographic range of a species is split during allopatric speciation, there is not a single rule for this splitting to occur; it might be symmetrical or highly asymmetrical depending on the speciation process (Losos and Glor 2003). Therefore, range size cannot be treated in the same way as

individual level traits (Maddison et al. 2007, Fitzjohn et al. 2009), and a new method should be developed to infer range size evolution and the effect of range size on diversification from phylogenetic trait distributions.

Spatial distribution of species: geographic range and diversity

Variation in species range size and underlying mechanisms

The spatial distribution of organisms is far from homogenous and understanding the causes of differences in geographic range size has become a central aim in ecological and evolutionary research. For example a multitude of species are present on the tropics, and the range sizes of them are rather small in contrast to temperate areas where the trend is reversed. Similar to other topics of biological interest, the study of the geographic range size of species and its variation must be approached through different spatial and temporal scales. One could consider those traits which enable organisms to adapt to local conditions promoting range expansion (Kirkpatrick and Barton 1997, Brauer and Geber 2002), linking in this way range size and environmental heterogeneity (Fjelds  et al. 1999, Pither 2003, Tello and Stevens 2010). Likewise to the ability to adapt to local, the niche breadth has been shown as important to define the range size (Pyron 1999) and at this point, the variation of local abundances across the range is thought as the key piece. For instance, population density declines from the center to the borders (Alleaume-Benharira et al. 2006) and movement of individuals plays a central role for gene flow to peripheral populations (Kirkpatrick and Barton 1997). The relationship between abundance and range size is apparently a prevalent pattern (but see Pyron 1999) but its extent is not straightforward: large-ranged species exhibit both high and low local abundances (Borregaard and Rahbek 2006), so the strength of this relationship varies depending on how restricted (or widespread) the species are (Borregaard and Rahbek 2006). Similarly, abundant species are likely to develop a high variation in range size according to Kirkpatrick and Barton's model (1997). Dispersal ability is also thought as important in explaining range size

variation. For instance, Lester and Ruttenberg (2005) found a positive relationship between larval duration (as a proxy of dispersal capacity) in reefs, although there is also evidence suggesting that this is not a general principle (Lester et al. 2007).

During the lifetime of a species, the range size changes and, although there is some evidence for a tendency of older clades showing larger ranges (Gaston and Blackburn 1997), the relationship between evolutionary age and range size can be highly nonlinear (Jablonski 1987). For instance, it seems that bird species expand quickly their range and then undergo a period of stasis prior to a decrease in range size (Webb and Gaston 2000). This pattern could match with the observation provided by the fossil record in molluscs which suggests a peak in range size around the middle age of species (Tietje and Kiessling 2013). Finally, variation in the relationship age and range size seems to be complex and depends on parameters such as speciation rates and mode of range split, in any case, a peak in range size is expected (Pigot et al. 2012).

Patterns in range size distributions and processes potentially involved

With a broader view, one would notice that certain trends appear repeatedly in different geographic areas and in different taxonomic groups. The striking difference in range size among species belonging to the same clade, could be framed in a latitudinal gradient where range-restricted species tend to be close to the tropics while the species' average range size increases towards the poles (i.e., Rapoport's rule). There is considerable doubt about this pattern because a similar outcome can be recovered by simple geometric restrictions (i.e., mid-domain effect, Colwell and Hurtt 1994); however there are examples where this pattern arises even when the mid-domain effect is taken into account as a null model to departure from (Ribas and Schoereder 2006).

Another interesting pattern is the frequency distributions of range size amongst species in the same clade that, in general, follows a strong right-skewed shape (Gaston 1998), where most of the species are range-restricted and a few species have large range sizes (Figure 1). This pattern is certainly widespread and

has been reported for primates (Eeley and Foley 1999), turtles (Hecnar 1999), copepods (De Troch et al. 2001), trees (Pither 2003) and snakes (Reed 2003) just to mention a few. An exception to this trend comes from marine organisms where range size distributions exhibit a bimodal shape (Mora and Robertson 2005, Scott et al. 2012). Gaston (1998) suggested an interplay among speciation, transformation (i.e., range dynamic) and extinction as potential mechanisms shaping range size distributions, based mostly on the relation between range size and probability of speciation/extinction. In this case, the information provided by paleontological evidence linking range size and evolutionary age could mislead conclusions because the data is scarce and might be biased (Russell and Lindberg 1988). Under the assumption of a relationship between abundance and range size, Gaston and He (2002) recovered the right-skewed pattern by using population dynamics, however the strength of the assumption is not always well supported (Borregaard and Rahbek 2006). Recently, Birand et al. (2012) simulated a dynamic model of dispersal and adaptation where species were able to coexist and showed differences in niche widths; these differential capacities among species allowed them to sort in space producing the right-skewed distribution in range size. The interaction among individuals has also been used to explain range size distributions. In Hui and McGeoch's model (2006), prey-predator dynamics in a metapopulation setting produced patterns similar to empirical ones. As we will see further, the species range size distribution is a metric that is unable to capture the entire complexity of spatial patterns of biodiversity and needs to be complemented with others. It remains to be explored to what extent the research previously conducted is able to explain them.

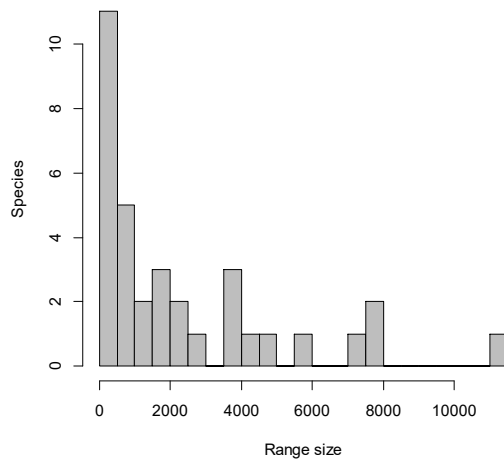


Figure 1. Frequency of geographic range sizes of Northern American sparrows (Emberizidae). Most of the species are range-restricted and a few species have large range sizes. This pattern is widespread and has been reported for several clades.

There are some studies which claim that range size distributions can be explained with combination of sample grain and species saturation in a fractal framework where the occupancy of a given species and its conditional probability is linked to a process of habitat division (i.e., bisection process) (McGeoch and Gaston 2002, Hui and McGeoch 2007).

Although these approaches recover mostly bimodal distributions which is not the most common pattern observed (only for marine organisms), they set the idea of patterns might be explained without invoking complex biological processes. That is what neutral theory accounts for and I will discuss it briefly in the next section.

The neutral case

According to the observations made by Jared Diamond (Diamond 1975), the co-occurrence of some species pairs are almost forbidden due to ecological

competition. When the debate about so called community ‘assembly rules’ took place (Diamond 1975)(Diamond 1975)(Diamond 1975)(Diamond 1975)(Diamond 1975)(Diamond 1975)(Diamond 1975) (Diamond 1975), ecologists wondered whether some apparently observed patterns in nature real required a special explanation or whether they were simply what we would expect by chance. They shuffled ecological data to produce the random expected frequency distribution for comparing the empirical data with, this procedure generates a null hypothesis which is a starting point to analyze biological phenomena (Gotelli and Ulrich 2012). In the same way, Hubbell’s neutral theory (2001) posits that before arguing evolutionary or ecological mechanisms behind patterns, we should first look at the expectation of simple processes which in turn is used as a benchmark. The central statement is that individuals, regardless of species are functionally equivalent. Of course, this contrasts with most of ecological literature where niche differentiation among species is the key factor, triggering an intense debate.

Nonetheless, the expectations of neutral theory fit surprisingly well in several patterns that have been subject of study by ecologists. Basic processes such as speciation, migration and dispersal are able to recover for instance, the relationship between richness and geographic area (Rosindell and Cornell 2009) as well as the relative abundances of species in an assemblage (Bell 2000). Thus, in case of existing biological mechanisms underlying those patterns, their complexity is not captured by the descriptors normally used and it is pointless to look for additional explanations (Rosindell et al. 2011). However, even when a pattern is consistent with neutral theory this does not mean nature is neutral, but simply that neutral processes can produce the same patterns which may be instead be interpreted as that these patterns are uninformative about true ecological interactions.

Recently Trejo-Barocio & Arita (2013) developed a model that incorporates the basic assumptions of neutral theory to generate species distributions. They used different parameter values for simulating the dynamics of the system and found that range size distributions under intermediate rates of both speciation and dispersal, are similar to empirical patterns. Evidence of neutral processes driving

species distributions at large spatial scales comes from this work, but the implementation of the model has some issues (e.g., low community size and number of individuals) that need to be addressed. These issues aside, another interesting insight about biodiversity patterns arises from Trejo-Barocio & Arita's paper which I point out below.

Species distributions, biodiversity patterns and the need of looking at different descriptors

If two species inhabit the same community, this means their geographic distributions overlap at the given spot. Richness in a given area, is the number of overlapping species geographic ranges and the species turnover (i.e., beta diversity) can be described as the relationship between total area and average range size of species (Routledge 1977). Likewise, the co-occurrence of species at a given site determines the community composition and the potential underlying mechanisms have been subject of intense debate. So far, we know that the co-occurrence patterns are non-random (Gotelli and McCabe 2002) and this finding deserves an explanation. Ultimately, how many assemblages the species are present in determines their range size. Thus the complex interaction between co-occurrence and biodiversity means that spatial distributions are not independent from biodiversity patterns and evolutionary and ecological processes.

While range size distributions can be recovered by neutral models (Trejo-Barocio and Arita 2013), predicting the distribution of species across sites is more challenging. Patterns of similarity among sites produced from neutral theory seem unrealistic (Trejo-Barocio and Arita 2013). The expected species co-occurrence under neutral models is also quite different from observed data. This suggests that even successful models previously proposed to explain range size distributions, might be unable to fully capture the spatial arrangements of species.

Ulrich (2004) wondered whether segregation or aggregation among species could emerge by simulating spatial distributions under a neutral framework and, according to his modelling, species are able to exhibit non-random co-occurrence

patterns. The values of the metrics he used to summarize the species co-occurrence expected by this stochastic process, do not resemble the empirical values found by Gotelli & McCabe (2002). The development of the model used by Ulrich (2004) has some points that would need to be addressed to be in line with Hubbell's (2001) theory. For instance, Ulrich's (2004) model explicitly ignores dispersal restrictions and fixes species.

From the above arguments it becomes clear that it is worth exploring how neutral theory might explain the spatial distribution of species, by considering simultaneously range size distributions and biodiversity patterns. A departure from the expectations of this stochastic approach, would encourage us to seek for an explanation on the grounds of biological mechanisms.

Biological interactions drive ecological patterns

The aggregation of organisms is not only dependent on the distribution of resources across space, but may be the outcome of organisms being either attracted or repelled by others. Species needs and the different ways to deal with them, determine that each species occupies a particular position within ecological space. However, an overlap among this suite of requirements could happen compromising the co-occurrence of species. Ecological competition is regarded as a fundamental force with the potential to exclude species from assemblages. The concept of competition has penetrated very deeply in ecologists' minds and a plethora of literature has appeared where competition plays a central role for the understanding of community assembly.

The amazing tree diversity in tropical forests and the fact that individuals of the same species co-occur less frequently than expected, have led to the Janzen-Connell effect (Janzen 1970, Connell 1971), which is an explanation based on ecological similarity among close relatives. It posits that the rate of seedling survival is lowest in the vicinity of parental/conspecific trees because they share host-specific pathogens or predators (Clark and Clark 1984). Recently this hypothesis has been extended beyond the species level: phylogenetic similarity

decreases survival probabilities, because pathogens and predators are more likely to attack species that have a similar (co-)evolutionary history. Liu et al. (2012) provided the first experimental evidence supporting this phylogenetic Janzen-Connell effect. In this case, biological interactions are regulating the patterns of co-occurrences of species via mechanisms other than (only) ecological competition. It remains to be studied what kind of phylogenetic and spatial patterns are generated by this mechanism, and conversely whether range size data can inform us about the strength of the phylogenetic Janzen-Connell effect.

Trait evolution and diversification processes: the geographic range size as an evolving trait

Geographic range as legacy

Evolutionary history has placed species in different paths, yet, different biotic and abiotic pressures are able to force organisms to develop similar behavior, physiology and morphology. However, the most common mechanism responsible for species similarity, is when they belong to related clades and those similarities are inherited during speciation. Several traits are passed to the daughter species which make them similar in requirements and capacities; some of these traits would be ecologically relevant and would determine the niche of that species. It seems that niche conservatism is a general pattern/process (Peterson, Soberón, & Sánchez-Cordero, 1999; but see Cardillo, 2015;) suggesting that niche evolution could take a long time. The authors reached such a conclusion by using environmental descriptors of the area of occurrence of one species to predict successfully the distribution of its sister species.

It might be expected that the geographic range sizes of species sharing an evolutionary history is similar if they are able to occupy similar areas. Webb & Gaston (2003) used the asymmetry of range sizes among sister species to conclude that there is not enough evidence for range size heritability. Nonetheless,

a pairwise method does not consider the entire species arrangement (i.e., phylogenetic tree) so important information about diversification process itself is not used. A better approach can be conducted by shuffling continuous trait values across the trees' tips and comparing the variance of the permuted independent contrasts to the variance of the real ones (i.e., phylogenetic signal *sensu* Blomberg et al. 2003). By doing so, Waldron (2007) found evidence of phylogenetic signal in range sizes of North American birds, which is in agreement with other studies where the entire phylogenetic tree has been used to test for range size similarity among close related species. Moreover, not only may range sizes be conserved, but the geographic position may also to a certain extent be inherited (Cardillo 2015).

Undergoing speciation or extinction as a function of character state

The forest canopy offers to animals new resources in the form of hard fruits (e.g., figs) which only can be taken by organisms capable of a strong bite. The development of a certain skull configuration by Stenodermatinae bats, has enabled them to take advantage of this available source with a relevant diet shift taking place. The incorporation of this key innovation leads to have an advantage in the new adaptive zone which in turn, it has happened to increase their speciation rate (Dumont et al. 2012).

Morphological traits are not the only type of features producing such an effect. For example, Gómez & Verdú (2012) found that mutualistic behavior leads to higher diversification as well. But not only is speciation affected by incorporating a new characteristic, but the lack of certain traits may also impact diversification. For instance, Polly (2014) found that the fitness of species might not be always improved by developing a new trait, and the absence of shifts in speciation rates could be the signature of this. However, he found that for those clades where the new trait was not present, the extinction rate was higher. Thus, diversification depends on character state and the phylogenetic arrangement of species could provide information about trait evolution and its influence on evolutionary

dynamics. Because most of speciation events occur in allopatry, a given relevant trait for diversification, ultimately must increase the chances of geographic isolation.

This interplay between characters and diversification can have different shapes mostly depending on the type of trait considered (Ng and Smith 2014). For instance, it is not only either the presence or absence of a given trait (e.g., the frugivorous bats example) which determines speciation or extinction rates, but for some traits, there are more states that may be exhibited by species. At least for plants, the dependence of diversification on reproductive structures linked to pollination is high (Fernandez-Mazuecos et al. 2013) but it seems there is a lack of relation between speciation and pollinator type (Forest et al. 2014). Finally the overall reproductive strategy in angiosperms (dioecy) correlates with higher diversification rates (Käfer et al. 2014). In the case of birds, the breeding system regarded as a multi-state trait was able to explain patterns in diversification variation (Marki et al. 2015).

The selection of traits potentially linked to diversification rests with the researcher's expertise on a given clade. Bouchenak-khelladi et al. (2015) assessed 27 plant traits which presumably could be related with high speciation rates, including both intrinsic (morphology and physiology) and extrinsic (vegetation associated) traits. They found that only a subset of the traits might be linked to diversification processes. This shows that the evolution of even ecologically important traits is not always associated with species diversification. For instance, variation in the number of vertebrae in reptiles promotes diversity in body shapes and ecological variety but is not related to species diversification (Bergmann and Irschick 2011).

Nonetheless many traits linked to the diversification process are not just categorical: they can also be continuous and must be treated in this way. The dependence of diversification rates on dispersal capacity seems straightforward, but recent research shows contrasting results. For instance among members of

buckwheat family, seed size evolution correlates with both high speciation and low extinction rates. Although a small seed can be a proxy of dispersal capacity, the mechanism of dispersal (by wind, water or animal transportation) is not related to diversification rates, and neither is seed dormancy (Kostikova et al. 2014). In the case of the well-radiated tropical clade Furnariidae (Ovenbirds and woodcreepers), the species exhibiting a high capacity of dispersion have at the same time a lower chance of speciation, which is explained through a constant gene flow (Claramunt et al. 2012). To what extent these results are generalizable is a further question. For example, ovenbirds and woodcreepers occur mostly in a relatively homogenous region (i.e., Amazonian basin) limiting the possibility of encountering new contrasting habitats even with high dispersal, preventing local adaptation and therefore speciation. Finally gene flow is also sensitive to the effects of geographic range size and shape, because large areas are more difficult to be well connected and speciation events could occur at the border where gene flow is low.

Body size is another trait that has received attention because it is thought to summarize several features of species' life history. Body size often correlates with demographic traits (e.g., generation length) which have been suggested as associated with speciation in tropical trees (Baker et al. 2014). Evidence in favor of a relationship with diversification has been found. For instance, in the case of snakes, body size increased the probability of speciation (Burbrink and Myers 2014). Likewise, a positive relationship was shown for salamanders (Machac et al. 2012) whereas in lizards of the genus *Liolaemus* the relationship between size and diversification is reversed (Pincheira-donoso et al. 2015). The relation could be more complex: the function which describes speciation rate and body size in primates is hump-shaped (i.e., highest speciation rate occurs at intermediate body size values, Fitzjohn, 2010). However evolutionary diversification depending on body size has been shown as non-existent in the case of colubrids (Pyrón and Burbrink, 2012) and carnivores (Machac, Zrzavy, Smrckova, & Storch, 2012).

Although biogeography can also gain important insights by trait-dependent diversification analysis, only a few studies have been conducted to date. For

latitudinal gradients, the diversification of *Amanita* mushrooms can be explained through its dependence on latitude (Sánchez-Ramírez et al. 2015). Pyron and Burbrink (2012) found that the evolution of the set of environmental conditions where species occur (i.e., climatic niche) impacts on speciation rate of ratsnakes; the same is true for salamanders and their metabolic dependence on temperature (Machac et al. 2012).

Models for trait evolution and their effect on diversification; the special case of range size

When a trait is thought to be relevant for speciation or extinction, the inference of its evolution must be coupled to the entire process of branching of a phylogenetic tree. Because the Binary-State Speciation and Extinction model (BiSSE; Maddison et al., 2007) is the baseline for similar models that deal with trait-dependent evolution, I am explaining it in more detail whereas the differences with more complex models will be discussed afterwards.

BiSSE is intended to simultaneously infer both the tree and the observed character states through a likelihood approach. The probability of switching between one state to another state (and vice versa) are two parameters that, alongside the speciation and extinction rates per state, comprise the six parameters of BiSSE. The procedure starts by evaluating the probability of a lineage showing a given character state (at a node) has evolved the character state at the tip of the branch. There are four possible events that could have happened during every time interval: 1) no state change, 2) state change. Because at the end of the branch we have just one lineage, speciation coupled with extinction (without state change) could have occurred as well. Thus 3) speciation and extinction of “left” lineage and 4) speciation and extinction of the “right” lineage. The time interval considered is so small that the possibility of two events happening within it is so small that is negligible. The probabilities of the four options are summed and are numerically integrated along the branch. At a node,

three probabilities must be multiplied: the probability of speciation, the probability of the left lineage evolved as in the tree and the probability of the right lineage evolved as in the tree.

The other important component of BiSSE is the calculation of extinction probability, which is the chance of a lineage with a certain trait present at given time, goes extinct before the current time. In a similar way to that mentioned above, there are four possible events that could have happened in a very small time interval: 1) Extinction of the lineage during time interval, 2) no change in state, then extinction, 3) change state, then extinction and 4) no state change, speciation and then extinction.

One step forward for the joint inference of trait evolution and diversification comes from Fitzjohn (2010), who developed the QuaSSE model which allows the analysis of quantitative (continuous) traits. Under Fitzjohn's (2010) model, several calculations are similar to those in BiSSE, but it is worth highlighting that character state transition probabilities are no longer needed. In this case, the evolution of the continuous trait is treated as a diffusion process (enabling it to be adapted to different models of trait evolution). This process comprises two components: the directional term which accounts for the expected rate of change through time (i.e., caused by selection for instance), and the diffusion term, which describes a random stochastic walk in trait space.

An important feature of QuaSSE is that at a speciation event, the character state is inherited by both daughter lineages and this makes sense for many traits, but it cannot be extended to all the cases. When regarding geographic range as a trait, what happens when speciation takes place is not as straightforward as other traits such as body size (Fitzjohn 2010). Daughter species will split in two the parental range and the size of the daughter's range will affect its probability of undergoing speciation or extinction. Ree, Moore, Webb, & Donoghue (2005) considered the possible options in which a range can be inherited under a discrete-area system. The trait itself does not evolve over time and dispersal among the

discrete areas is taken into account. The GeoSSE model (Goldberg et al. 2011) deals with traits which are transformed by the speciation process where at least one of the daughter species has a different state than the parent. The GeoSSE model is also framed in a discrete-area system where range size decrease happens via contraction (i.e., the trait evolves along a branch) and speciation, whereas range expansion occurs by dispersal. The next step, considering geographic range size as a continuous trait instead of a discrete one, would be to link the conceptual ideas from Goldberg et al (2011) where there is an obligate state change at speciation event, with the framework from Fitzjohn (2010) which is intended to account for character evolution along a branch.

Is trait-dependent diversification consistent with trait frequency distributions?

One implicit assumption of trait-dependent diversification analysis is that species can be wiped out when they exhibit character states which are not favorable from an evolutionary standpoint. On the other side of the coin, some species boast the “right” character state which would boost the probability of speciation. I will not go deeper into whether this is species selection (species sorting) because its definition goes beyond the scope of my research. I will just say that selection acts on certain traits in organisms and that some of those traits can be scaled up and become species features: this is the combination of trait values of the individuals belonging to a given species (i.e., aggregate traits, Jablonski (2008)).

The example used by Fitzjohn (2012), body size evolution in primates, to demonstrate the utility of his model, shows how speciation rates varies as function of character state. He also shows the frequency distribution of body size among members of the clade. The highest speciation rates according to the best fitted model occurs around 2.5-13.4 kg and this coincides with the modal class of body size of the extant primate species. However this is not always the case: there are studies where the frequency distribution of a trait on extant species does not match with the expectations of the function describing the relationship trait-speciation rate. Examples of both conditions will be briefly discussed in the next paragraphs,

evoking two questions: What are the mechanisms that causes that mismatch? Can they be inferred by combining trait frequency distributions and trait-dependence diversification analysis?

The diversity of *Amanita* mushrooms exhibits an increase of richness in northern latitudes, but the best fit function describing speciation rate as a function of latitude shows a peak around 27°, which is not the peak of *Amanita* diversity (Sánchez-Ramírez et al. 2015). Likewise, the relationship between dispersal capacity and speciation in passerines is not completely in line with the modal class of dispersal ability, but the trend of higher speciation rates at low dispersal is somehow reflected on the trait distribution (Claramunt et al. 2012).

For lizards, Pincheira-donoso et al. (2015) found that a linear negative function is the best at describing speciation rate as function of body size, but the distribution of body size is bimodal: large-bodied species are common. The body size distributions (normal-like) are not in agreement with the body size-speciation rate relationship (linear) for colubrids (Burbrink and Myers 2014). Finally, the histogram of ratsnakes species across a gradient summarizing environmental complexity (Figure 2), is left-skewed and this shape is different from the bell shape function resulting from trait-dependent diversification analysis (Pyrón and Burbrink 2012).

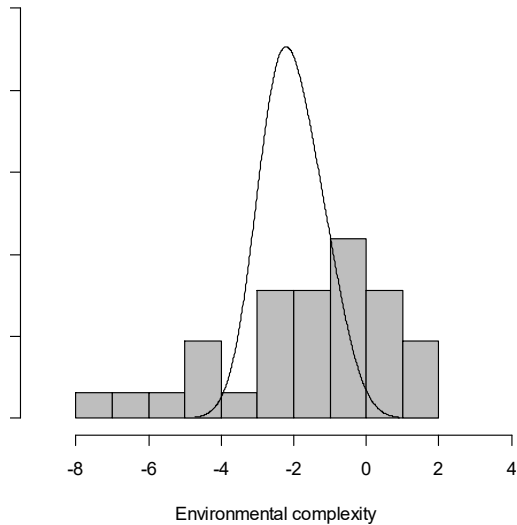


Figure 2. Trait-dependent diversification is not always in line with the trait frequency distribution among extant species. The black line depicts speciation-rate as a function of trait value in Lampropeltini snakes while the histogram represents the frequency of the trait.

Important traits for diversification

The way traits shape populations and vice versa can be extended to larger time scales to start thinking how these traits impact diversification. For instance, in phytophagous insects, small body size makes them prone to speciation (via sensitivity to barriers) and at the same time allows a larger population size, which in turn prevents the species from extinction (Jablonski 2008). The outcome of such a fortunate combination is high speciation rate and low extinction rate.

Besides morphological features, there are other relevant traits for diversification, in the case of land snail, their peculiar dispersal capacity is a good example. Snails do not move a lot. The energy expenditure of snail movements may be around twelve times the energy costs for an animal of the same size (Ozgo and Bogucki 2011). The dispersal ability of snails is different from plants where the restriction occurs only during adult stage: plants are designed to send the offspring (seeds) away to distant places via wind, water or animals. Land snails have no

such strategies and hence density-dependent processes seem more important in snails whose offspring are raised in the surroundings of parents. To what extent the low dispersal capacity of snails influences its diversification, remains to be investigated. Claramunt et al. (2012) claims that low dispersal capacity promotes speciation, finding that this could be in line with the outstanding local richness of microsnails. As an aside I note that Claramunt and co-authors assessed flying capacity (that could be translated to home range) rather than the spatial relationship between parent-offspring.

How do the patterns of co-occurrence of closely related species in land snails (Cowie 1992) arise? The complex patterns of sympatry of closely related land snail species and additional evidence, suggest that sympatric/parapatric speciation is likely in this group (Cowie 1992, Greve et al. 2012). Nonetheless secondary contact has been argued as well (Schilthuizen et al. 2006). Independently of the speciation mode, the co-occurrence of evolutionary relatives poses the question: what are the ecological and evolutionary mechanisms enabling co-occurrence? Resource partitioning and ecological diversification have been shown as important for allowing species coexistence (Cowie 1992, Chiba 2004) and perhaps this explains the micro-scale sympatry in some genera (Nekola et al. 2009). Although ecological competition among land snails has been considered to be less important role (Cameron 2013), a few cases of character displacement (i.e., phenotypic variation of species only in sympatry) have been documented in *Mandarina* (Chiba 2004) and *Partula* (Murray and Clark 1980). In both cases, the body size difference between species co-occurring at the same communities are larger.

In this way, it can be said that body size in land snails is closely associated to population dynamics and potentially linked to evolutionary diversification. Likewise, processes happening at ecological scales correlate with body size. The question of how ecological pressures drive body size evolution and therefore influence the outcome of diversification, challenges an integration of evolutionary and ecological approaches.

Summary

The location of organisms determines the set of environmental factors which they must deal with. Also the distance among organisms impacts individual performance through density-dependent processes or biological interactions. The way in which populations are connected to each other determines gene flow variation, and even in a continuous high-cohesive population, the spatial location of individuals coupled with dispersal ability could explain genetic heterogeneity. But it is not only at small time scales where organisms' geographic positions are important, but the birth and death of species are also influenced by this. Regarding again the relationship between spatial distribution and gene flow, speciation is likely to take place at the most distant regions of the species' ranges via genetic isolation. However, there are other mechanisms apart from population connectivity that can link geography and diversification. The size of the geographic range could be related to the probability of both speciation and extinction and this must be reflected in phylogenetic trees. On the other hand, because the most common mode of speciation is allopatric, those characters which are thought as relevant for trait-dependent diversification, must ultimately promote geographic isolation. Evolutionary and ecological processes have occurred without any witness, yet, geographic information and relatedness among species are the only traces that have been left behind to elucidate them.

Research questions

All these considerations lead me to conjecture that species range distributions and trait evolution contain information on the mechanisms shaping ecological communities, including ecological interactions as well as macro-evolutionary drivers. To study this in more detail, I want to ask the following questions:

- 1) What are the expectations of neutral theory on range size distributions and co-occurrence patterns?

2) What is the influence of a) diversity dependence and b) strength of species interactions (based on their ecological similarity) such as the Janzen-Connell effect and competition, on range size distributions, and on regional richness and species turnover?

3) Can we infer the influence of range size on speciation and extinction rates, and range size evolution from phylogenetic trees and range size data of species constituting an ecological community?

4) What are the differences of the models of range size expansion, its influence on diversification, and biological interactions for hotspots of richness and endemism? And have the values of species richness and number of endemics in hotspots changed through time?

5) What mechanisms are responsible for the mismatch between the expectations of trait-dependence diversification and the frequency distributions of extant species' traits?

Approaches

RQ1. I will develop a spatial model under the assumptions of neutral theory. Range size distributions, site richness and co-occurrence patterns will be the outcome of the model.

When it comes to develop procedures to test evolutionary or ecological hypotheses, one problem frequently encountered by researchers during running simulations, is the restriction of both computation capacity and time. I will use the coalescence approach which is a technique applied to neutral theory (Rosindell et al. 2008) that allows us to speed up the simulations by focusing only on the sample we look at. I will randomly place individuals into a world (the model is spatially explicit) with a fixed position. At this point one can define communities, so we would know which individuals inhabit each community. The goal of the coalescence process is then to determine the species identity of each one of the

individuals in the sample. At the beginning, all individuals belong to the same species and at the end of the process, one can analyze how the species are distributed in the world and communities (i.e., the original positions). The neutral process in this case is based on two events: dispersal and speciation and the interaction of both shapes the final biodiversity patterns. Different from traditional simulations that run forwards in the simulated time, the coalescence approach goes backwards: we first define the final distributions of individuals (species identity is unknown) and the simulations will reconstruct what happened in the past. Speciation rate needs to be set as well as dispersal capacity which is defined according to a given distribution (Figure 3). In each time step, one individual of the sample is randomly chosen and its ancestor (because time goes backwards) is selected in the world according the dispersal capacities defined by the user. If the ancestor belongs to our sample, we know now that (at least) those two individuals belong to the same lineage, then we can continue with only one of them for the next times steps and there is now a smaller sample to track. By letting the procedure run, eventually all the individuals would “merge” into a single lineage. However, speciation takes place in the neutral theory and to incorporate this, we need to allow a probability of undergoing speciation at every time step. When speciation happens at a given lineage, all the individuals that had merged into that lineage, belong to a species which is different from the rest.

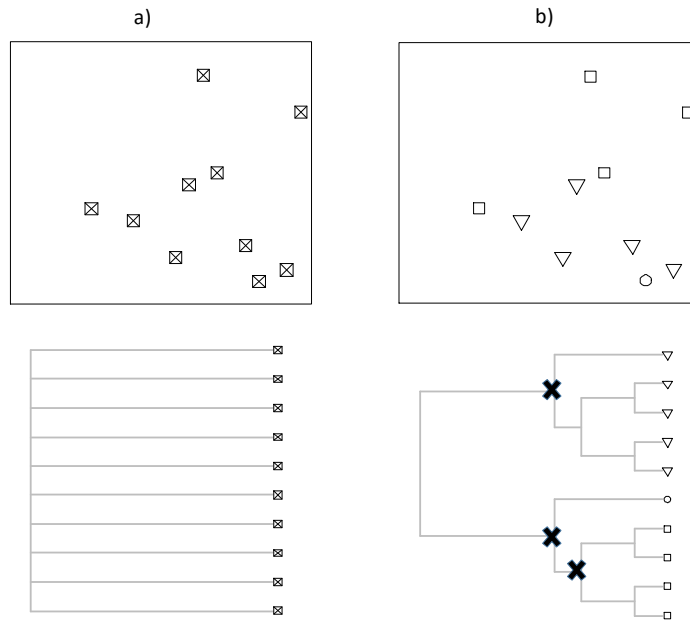


Figure 3. Neutral theory using a spatially-explicit coalescence approach. At the beginning of the run, all individuals belong to the same species (a) and at the end of the process, one can analyze how the species are distributed across the world (b). The crosses in b indicate when speciation took place in this backwards simulation.

RQ2. I will use a species-level approach where species expansion starts from one single population. The range expands on a grid, and each grid cell tracks the number of species on it. I will set different carrying capacity values which determine the maximum number of species, limiting the immigration and thus range expansion. Additionally, I will define a gradient where carrying capacity varies across the simulated world. When a steady state is reached, both the range size distribution and regional richness will be calculated

In addition, I will design a spatially explicit model where the probability of successfully expanding to the contiguous area depends on a) potential competition intensity or b) the strength of the phylogenetic Janzen-Connell effect. In a) the probability of occurring in a new area would be a function of phylogenetic similarity

between the species under expansion and the set of species already present in the area. I will use different parameter values of dispersal and competition strength limiting species expansion to compare the simulated frequency distribution to those observed in nature for several taxa. In b) the underlying idea is that colonization probability varies with the strength of phylogenetic effect. An important stochastic component is represented by both random deaths and speciation events. By setting different values of the strength of the Janzen-Connell effect, I will study the variation in range sizes and geographic range distributions. Since the species distribution might not be cohesive, I will evaluate the internal structure of the simulated species ranges through fractal dimension analysis (Maurer 1994).

In both cases I will describe species richness in local assemblages. Moreover I will compare community composition among local communities to find out to what extent biological interactions might explain species turnover, by setting different values for the strength of biological interactions. I will vary the size of the region to explore the effect on all these diversity patterns.

I will extend the model in b) to include macro-evolutionary processes, where the probability of speciation and extinction is not random, but is linked to the spatial distribution of species. I will explore by simulations how range size and connectivity between populations determine the probability of speciation or extinction.

RQ3. Given a phylogeny and species range size information, I will use a likelihood approach to estimate parameters such as range expansion and contraction rates and asymmetry of range size splits at speciation events. The development of this method will allow me to determine the effect of range size evolution on speciation and extinction. I will take as a base the approach proposed by Fitzjohn (2010). While range size is treated as a discrete character in Goldberg et al. (2011) and Ree and Smith (2008), I will model it as a continuous trait. However at the moment of speciation, range size can be passed on to the daughter species in a variety of ways which I will explore. I will also study the performance of this new method by testing the probability of Type I error (Rabosky and Goldberg 2015), and the statistical power which could be low as a

consequence of small sample size or very dissimilar character state ratios (Davis et al. 2013). I will select well-resolved phylogenies, such as the comprehensive avian phylogeny provided by Jetz et al. (2012) and the geographic information of species will be collected from NatureServe (Ridgely et al. 2007) and BirdLife International, where the distribution of several taxa is already digitalized and available. I will try to allow for incomplete phylogenies by adopting approaches like Fitzjohn et al. (2009).

The model will be a modification of the QuaSSE model. On a branch, the range size evolution will comprise both diffusion and a directional terms (similar to Fitzjohn's model) which allows to include stochasticity in its evolution. There is an important difference with QuaSSE that we must take into account that the trait value at moment of speciation is instantaneously reduced because a portion of it is inherited to the daughter species. Another important difference with standard QuaSSE is that range size equals to zero, extinction must occur.

At the node the range size should be divided among the daughter lineages.

RQ4. I will compare expansion rates using the likelihood method developed in RQ3 for the set of species occurring in hotspots and species outside of these areas. To test whether the current hotspots possess both high diversity and geographically rare species in the past, I will perform two analyses. First, I will estimate parameters of the model in RQ3 and run simulations with these parameters yielding information on ancestral ranges sizes for the species inhabiting those hotspots. Second, by using the phylogeny of those species, I will infer the number of species through time under a model of diversity-dependence (Etienne et al. 2012). Taken together, an estimation of species richness and average range size over time will be possible.

RQ5. Ectotherms are particularly sensitive to environmental conditions because of their temperature dependence which limits their geographic distributions. The

temperature range in which lizards are comfortable and perform all the activities in a normal way is called Thermal Tolerance (ThT). High values of this trait enable lizards of the South American genus *Liolaemus* to inhabit different regions (because of their climatic flexibility) causing large geographic range (Cruz et al. 2005). By experiencing an increase in distribution area, species are more prone to speciation. In this way, it is expected that ThT is related to speciation rates in a positive manner.

The distribution of individuals is not the only issue affected by temperature but their running ability, an important factor which leads to the survival of lizards (e.g., ability to escape from predators). Because there are physiological constraints relating animal movements and energy expenditure, *Liolaemos* with broad thermal tolerance, exhibit a poor locomotor performance (Bonino et al. 2015). Species with high thermal tolerance, are able to settle in areas under different environmental regimes, but this same feature could compromise their local performance. In this way, an optimal trait value for evolutionary purposes (i.e., speciation) is not the same for an ecological standpoint (i.e., performance). Could this be reflected in frequency distribution of this trait among *Liolaemus*?

I will simulate the evolution of a clade where the trait evolves over time and the probability of speciation and extinction are functions of the character state. The trait evolves in a stochastic way (pure Brownian motion) or under an Ornstein-Uhlenbeck process where the trait evolves slowly towards either high or low state. The frequency of diversification events (time elapsed) will be taken from a distribution (like Poisson) and when an event takes place, the probability of speciation and extinction will be dependent on the trait value. Two set of simulations will be carried out: 1) speciation is fostered by large trait values (i.e., positive relationship between speciation and trait) and 2) speciation is hindered by large trait values (i.e., negative relationship between speciation and trait). The simulation will be stopped when the number of species is similar to the *Liolaemus* clade size and the current character state of extant species will be stored. Using the simulated phylogeny and trait values, a QuaSSE analysis will be conducted.

The outcome of the trait-dependent diversification will be compared with trait distribution and the disagreement would be measured. I will repeat this procedure as many times as computationally feasible.

Timetable

1 st year	2 nd year	3 rd year	4 th year
<i>Spatially explicit model RQ 2 and 3</i>	<i>Neutral-Coalescence model RQ 1</i>		
	<i>Likelihood estimation of range size evolution RQ 3</i>		
		<i>Mismatch in trait evolution RQ 5</i>	
			<i>Hotspot analysis RQ 4</i>
			<i>Writing of introduction and general conclusions.</i>

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