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Integrating selection, niche, and diversification into a hierarchical conceptual framework

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Abstract Recently, new phylogenetic comparative methods have been proposed to test for the association of biological traits with diversification patterns, with species ecological "niche" being one of the most studied traits. In general, these methods implicitly assume natural selection acting at the species level, thus implying the mechanism of species selection. However, natural selection acting at the organismal level could also influence diversification patterns (i.e., effect macroevolution). Owing to our scarce knowledge on multi-level selection regarding niche as a trait, we propose a conceptual model to discuss and guide the test between species selection and effect macroevolution within a hierarchical framework. We first assume niche as an organismal as well as a species' trait that interacts with the environment and results in species-level differential fitness. Then, we argue that niche heritability, a requirement for natural selection, can be assessed by its phylogenetic signal. Finally, we propose several predictions that can be tested in the future by disentangling both types of evolutionary processes (species selection or effect macroevolution). Our framework can have important implications for guiding analyses that aim to understand the hierarchical perspective of evolution.

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Introduction

After the modern evolutionary synthesis that unified the ideas of Mendel and Darwin in the 1930s and 1940s, evolutionary dynamics through deep time began to be thoroughly discussed under the mechanism of natural selection (Simpson 1944). However, the focus remained on explaining macroevolutionary patterns as a result of within-species, microevolutionary processes (Gould 1982). Some authors questioned this classic perspective of selective process acting at the organismal level (i.e., organisms within species), considering it insufficient to explain macroevolutionary patterns, and suggested an expansion to the modern synthesis (Eldredge and Gould 1972). One aspect of this expansion was based on a hierarchical view of evolution, which considers processes acting at different levels of biological organization and emphasizes the effects of scale and hierarchy to improve our understanding of the history of life (Gould 1982; Jablonski 2007).

Organic evolution by means of natural selection could happen through the environment selecting organisms with certain traits (Darwin 1859), which is traditionally understood as a population-level process. However, such Darwinian mechanism could also happen at any level of the biological hierarchy, from genes to higher taxa, given that certain conditions are met (Jablonski 2008). This hierarchical expansion of the evolutionary theory is logically possible if the units of selection can be shown to have traits presenting three basic criteria: (i) variability, (ii) heritability, and (iii) interaction with the environment resulting in differential reproduction (Lewontin 1970).

Under this view, selective process could happen at the species level (i.e., species selection) if species present traits that are variable, heritable, and promote differential speciation and/or extinction across lineages (Stanley 1975; Rabosky and McCune 2009). Although theoretically possible and increasingly accepted, there is still ample debate around species selection as an evolutionary force, with two main topics of debate: whether species' traits can be downscaled to the organismal level and whether diversification patterns result from microevolutionary or macroevolutionary processes (Lieberman and Vrba 2005; Jablonski 2008; Myers and Saupe 2013). The first issue revolves around the consideration of species' traits as "aggregated"—organismal traits—or as traits exclusively "emerging" at the species level (Lloyd and Gould 1993). On one hand, aggregate traits can be represented as descriptive statistics (e.g., sum or mean) of a certain organisms' trait of a given species, with some examples being body size, dispersal capabilities, or trophic levels (Jablonski 2008). On the other hand, emergent traits are species' characteristics that only occur at the species level and cannot be summarized by descriptive statistics of organisms' traits; some examples are geographic range, sex ratio, and genetic population structure (Jablonski 2008).

The debate on whether diversification patterns are mediated by microevolutionary and/or macroevolutionary processes hinges on the distinction between upward and downward causations (Lieberman and Vrba 2005). Upward causation represents the selective process acting over organismal-level traits that influence diversification at the species level, a process also known as effect macroevolution (Vrba and Eldredge 1984). An example of effect macroevolution can be the interaction of the environment with organism's body size determining differential diversification across lineages (Jablonski 2008). However, it is important to highlight that upward causation will not always necessarily affect species-level evolution (Vrba and Gould 1986). Downward causation, on the contrary, represents selective process acting upon species traits that influence diversification at the species level as well as birth and death rates at the organismal level. This process is also known as "strict-sense" species selection (hereafter, simply species selection) (Jablonski 2008). An example of species selection can be the interaction of the environment with species' geographic range resulting in differential diversification across lineages (Vrba and Gould 1986; Jablonski 1987).

A first attempt to disentangle between effect macroevolution and species selection is to determine whether the biological trait under selection is aggregated or emergent (Jablonski 2008). If the trait is aggregated, effect macroevolution is more likely the main macroevolutionary process. Otherwise, if the trait is classified as emergent, species selection must be necessarily the main evolutionary process behind macroevolutionary patterns (Jablonski 2008). However, it is possible that a given aggregated trait that increases organismal-level fitness could also decrease species-level fitness (or the other way around; see Diniz-Filho 2004). That is, an asymmetry between levels may arise from the interaction of different level traits with the environment. An example of this "cross-level" conflict could happen with body size. Large organisms are traditionally assumed to present increased fitness owing to higher competing capabilities and/or environmental tolerances than smaller organisms (Maurer 1998). At the same time, species composed of large organisms require larger areas (geographical ranges) to satisfy their energetic needs and maintain viable populations compared to small organisms (Marquet and Taper 1998). Consequently, species composed of large organisms may have higher chances of extinction under a fluctuating environment than species with small organisms (Diniz-Filho 2004). Therefore, we believe that disentangling effect macroevolution from species selection is not as straightforward as simply defining whether a species' trait can be reduced or not to the organismal level.

Recently, with the advancement of phylogenetic comparative methods, several models have been formulated to test for statistical associations between biological traits and differential speciation and/or extinction (Maddison et al. 2007; Pyron and Wiens 2013; Morlon 2014; see a critic to these methods in Rabosky and Goldberg 2015). However, the majority of studies using such trait-dependent diversification models have not explicitly discussed the abovementioned topics such as trait reducibility, selection at different levels, or cross-level conflicts (but see Goldberg et al. 2010). For instance, some studies have tested for an association between ecological niches and diversification patterns (Kozak and Wiens 2010; Price et al. 2012; Rojas et al. 2012; Pyron and Wiens 2013; Title and Burns 2015, Rolland and Salamin 2016), but none of them explicitly tested or discussed whether effect macroevolution or species selection was the main process driving diversification patterns.

Our main goal here is to develop a conceptual framework to disentangle between effect macroevolution and species selection through the identification of the biological level at which natural selection is more important to determine diversification patterns. In addition, our framework also aims to evaluate the existence of a potential conflict between levels. We constructed our framework based on Lewontin's triad—variability, heritability, and interaction—acting over an organismal-level trait as well as over a species-level trait. We focus on the ecological niche as the biological trait under selection owing to several studies which already discussed the association of this trait with clade dynamics (see Title and Burns 2015). We first provide a brief overview of different interpretations on ecological niche and then describe our working concept of ecological niche as an aggregate trait that interacts with the environment. Later, we discuss how the conceptual and methodological advances on niche evolutionary dynamics could be useful to understand niche heritability.

Finally, we build our conceptual framework under several premises to provide a set of predictions that can help to identify effect macroevolution or species selection as the main evolutionary process behind diversification patterns.

Niche

One of the most intensively studied but yet controversial properties of species is their niche (McInerny and Etienne 2012; Soberón 2014). Niche can be broadly defined as an abstraction of the species' relationship with the environmental conditions, but, despite or perhaps because of its long history, there is still considerable debate over the meaning of the term "niche" (McInerny and Etienne 2012). Indeed, it is currently accepted that the niche can be composed of different variables (e.g., "scenopoetic" or "bionomic"; Hutchinson 1978; Soberón 2007), can have different "components" (e.g., fundamental or realized; Hutchinson 1957), and can be described at different biological levels (e.g., organism or species level; Bolnick et al. 2003; Myers and Saupe 2013).

George Evelyn Hutchinson formalized the niche concept as the set of scenopoetic and bionomic variables that permit species to exist indefinitely (Hutchinson 1978). Scenopoetic variables are composed of abiotic properties of the environment such as temperature or precipitation, whereas bionomic variables are composed of different types of resources such as preys, sexual mates, or nest sites whose availability is associated with biotic interactions like competition, mutualism, parasitism, or predation (Hutchinson 1978; Soberón 2007). Moreover, he demonstrated through a set-theoretic representation that two species that occupy similar areas in the geographical space have necessarily to occupy different areas in the environmental space (Hutchinson 1957). In other words, each species has its own set of environmental conditions in which it can exist indefinitely: its fundamental niche. Moreover, owing to negative biotic interactions, each species occupies just a part of available environmental space: its realized niche. Another important contribution of Hutchinson's work was the recognition of an interface between the geographical (G) and environmental (E) space (Colwell and Rangel 2009). The geography-environment duality is asymmetrical because different regions in the G space represent specific regions in the E space, whereas the opposite is not necessarily true. That is, there is a one-to-one relationship from G to E space but a one-to-many relationship from E to G space (Soberón and Nakamura 2009). Besides theoretical advances in understanding the interaction between both spaces, the geography-environment duality has also had important implications in biogeography and macroecology. For instance, this theoretical reasoning highlights that the geographical distribution of a species is ultimately determined by three main aspects: the abiotic conditions defining its fundamental niche, biotic factors defining its realized niche, and the regions accessible to dispersal (see the BAM diagram of Peterson and Soberón 2012; Soberón and Peterson 2005).

More recently, Soberón (2007) proposed the separation of the niche concept on the basis of spatial scale. He proposed the distinction between Grinnellian and Eltonian niches, with the first concerning broad-scale scenopoetic variables defining the conditions (e.g., climatic variables) that a given species can occupy whereas the second referring to bionomic variables representing resources at the local scale that a species can consume (Soberón 2007). This separation allows disentangling local from regional processes and has direct implications in the growing literature that focus on species' niches to answer macroecological and biogeographical questions (Colwell and Rangel 2009; Peterson and Soberón 2012).

Niche as an aggregate trait

All niche concepts discussed above are based on the idea of the niche being an abstraction of a species' relationship with its environment. Consequently, any attempt to consider the niche within a conceptual framework of species properties being influenced by natural selection (like ours) may suffer from circularity. This circularity may arise because, on one hand, natural selection would act through the interaction of the environment with the species' trait, in this case its niche. But, on the other hand, niche is already defined as the relationship of a species with its environment. Thus, to avoid this potential issue, we explicitly consider the species' niche as a biological trait that can be inherited and whose interaction with the environment might provide differential fitness. Under this view, niches are potentially subject to natural selection caused by the environment as any other traditional biological trait.

Is the niche an aggregate or an emergent "trait"? Niche is traditionally interpreted as an aggregate trait, where species' environmental requirements can be reduced to organismal (Simpson 1944; Vrba 1987; Jablonski 2008). Currently, some authors interpret—implicitly or explicitly—niche as a species-level, emergent trait (Losos 2008; Wiens et al. 2010; Myers and Saupe 2013), while others still maintain the traditional interpretation of the niche as an organismal-level, aggregated trait (Bolnick et al. 2003; Araújo et al. 2011). Such dichotomy is associated with the variables used to determine the species niche. Authors favoring the niche as an aggregate trait focus on Eltonian niches, in which the niche is defined, for example, as dietary items that organisms consume and can be used to characterize organisms either as generalists or specialists (Bolnick et al. 2003). This interpretation of the niche as an aggregate trait relies on optimal forage and quantitative genetic theory (Araújo et al. 2011). Alternatively, authors favoring the niche as an emergent trait focus on Grinnellian niches, defining the niche as the set of abiotic conditions that species are adapted to (Pyron and Wiens 2013). However, most of these authors do not explicitly equate Grinnellian niches with emergent, species-level traits. An important exception is Myers and Saupe (2013), who explicitly defined the Grinnelian niche as an emergent trait of species. For them, any association that organisms have with abiotic conditions should be interpreted as environmental tolerance of the species as a whole and not as an intrinsic organismal trait (Myers and Saupe 2013).

Here, we assume the niche—whether Eltonian or Grinnellian—as an aggregate trait of the species. We believe that this consideration is the most operational for the advancement of macroevolutionary theory. According to Jablonski (2007), an emergent trait is a feature of a given biological level whose evolutionary consequences are not affected by how the feature is generated at lower biological levels. However, as we are going to elaborate in the final part of this paper, organismal-level niches can also affect diversification patterns as well as the species-level niche. Consequently, we argue that niche should be interpreted as an aggregate rather than an emergent trait and that its variability can be quantified (first element of Lewontin's triad).

Niche evolutionary dynamics and heritability

The second element of Lewontin's triad for the occurrence of natural selection is its trait heritability. Traditionally, researches used simple correlation of a given trait—e.g., range size—between ancestor-descendant species pairs to test for trait heritability (Jablonski 1987; Webb and Gaston 2003). With the high advancement of phylogenetic comparative methods (Harvey and Pagel 1991; Pennell and Harmon 2013), trait heritability is now being tested within an explicit phylogenetic perspective and with more sophisticated methods (Machac et al. 2011; Cardillo 2015).

Phylogenetic comparative methods were traditionally used to understand traits' evolutionary dynamics—such as whether a trait is conserved or labile over time—rather than heritability (Freckleton et al. 2002; Pennell and Harmon 2013). For example, to test whether closely related species resemble each other more than expected by chance in relation to their ecological attributes (i.e., niche conservatism (NC); Pearman et al. 2008), authors have quantified the phylogenetic signal of species niches (Wiens et al. 2010). In these studies, a statistically significant signal was interpreted as evidence for niche conservatism, whereas an absence of a signal was interpreted as the niche being a labile trait. However, this analytical framework has important drawbacks. For instance, there is no agreement as to what extent should be the level of signal to assume conservatism (Losos 2008; Wiens 2008); the signal itself may be scale-dependent both in spatial and temporal terms (Cavender-Bares et al. 2009) and might present phylogenetic non-stationarity (Diniz-Filho et al. 2010, 2015). Finally, there is evidence that different evolutionary processes could result in the same levels of phylogenetic signal (Revell et al. 2008).

Despite these drawbacks, we still consider phylogenetic comparative methods to be very useful in testing for niche heritability (see Machac et al. 2011; Cardillo 2015). However, it is necessary to define the ecological niche as a species' property and then interpret its phylogenetic signal as representing heritability instead of evolutionary dynamics. Phylogenetic signal could represent heritability because, under a neutral evolutionary model (e.g., Brownian motion), trait variability among lineages is linearly correlated with time (Felsenstein 1985). The basic assumptions underlying this pattern are a deterministic component (i.e., genetics), which constrains trait variability, and a stochastic component (i.e., genetic drift), which permits trait variability to increase proportionally with time. Thus, the genetic component constraining trait variability could be interpreted as similarity by descent, which, in turn, can be a direct surrogate for heritability. Other processes such as a selective process with a very rapid fluctuation through time could also determine a phylogenetic signal expected under Brownian motion (Revell et al. 2008). Nevertheless, this alternative process does not invalidate the use of the signal as a surrogate of heritability since heritability is also a basic assumption of natural selection (Lewontin 1970).

Conceptual framework

We have already argued how species niche could be understood as an aggregate trait that possesses variability, can be downscaled to the organismal level, and may present heritability. Based on these conditions and assuming Lewontin's third premise—niche interacts with the environment resulting in differential reproduction, we propose a conceptual framework to evaluate whether effect macroevolution or species selection acting upon species niches is more important to mediate diversification patterns. First, we define the system that we were interested to understand. Second, we establish which property of the system was more important for testing and disentangling between causal processes (effect macroevolution or species selection). Third, we determine which causal processes were the main drivers of the system's property. Fourth, we identify the premises of the potential causal processes. Fifth, we propose testable predictions. Finally, we highlight how this conceptual framework could be important for future analyses to understand which evolutionary processes are more important to explain diversification patterns.

The system that we are interested to explain is the phylogenetic tree of a given taxonomic group. The specific property of this system that we are interested in is the diversification pattern, which represents the balance between speciation (λ)

and extinction (μ) rates. We assume natural selection as the general mechanism shaping the phylogenetic tree and the ecological niche as the biological trait under selection

The ecological niche is composed of the values of the environmental space that each species and organism is adapted for. For simplicity, we assumed a one-dimensional E space which can be a variable representing a given niche variable (i.e., scenopoetic or bionomic). Since niche is an aggregate trait, species as well as organisms present niche properties (Fig. 1). We considered two niche properties: breadth and value (Quintero and Wiens 2013). Niche breadth is the set of environmental values that each species and organism is adapted to, whereas niche value is the environmental value where each species and organism reaches its highest fitness. Thus, there are three types of species in terms of niche breadth: generalist species composed of generalist or specialist organisms (GEN-gen or GEN-spe, respectively) and specialist species composed of specialist organisms (SPE). We did not assume specialist species with generalist organisms (i.e., SPE-gen) because the organisms of such species would always be specialist when compared to organisms of generalist species. In terms of niche value, specialist species and organisms can establish a restricted niche value, whereas generalist species and organisms tend to establish different niche values within their niche.

Since we assumed species niche as an aggregate trait, two evolutionary processes could explain a diversification pattern: effect macroevolution or species selection. On one hand, if effect macroevolution is the main process, the environment acts only upon organisms' niche breadth resulting in differential fitness among organisms. Consequently, this microevolutionary process is scaled up to the species level (i.e., upward causation) resulting in differential diversification. Thus, we assumed that if GEN-gen or SPE species presents higher fitness than GEN-spe species, effect macroevolution is the main process driving diversification patterns. Because the former species present the same niche breadth at both biological levels (species and organisms), whereas the latter species present different niche breadths between species and its organisms, therefore, it is more parsimonious to infer effect macroevolution rather than species selection as the main causal process. On the other hand, if species selection was the main process, this would necessarily generate a cross-level conflict between fitness associated with niche breadth. Cross-level conflict occurs when a given niche breadth (e.g., specialist) at the organismal level results in high organismal fitness, but a different niche breadth (e.g., generalist) at the species level also results in high species fitness. Thus, we assume that if GEN-spe species present higher fitness than GEN-gen or SPE species, species selection is the main causal process driving diversification patterns. Since we assumed niche as an aggregate trait, the absence of cross-level conflict means that only effect macroevolution can be raised to explain the diversification pattern.

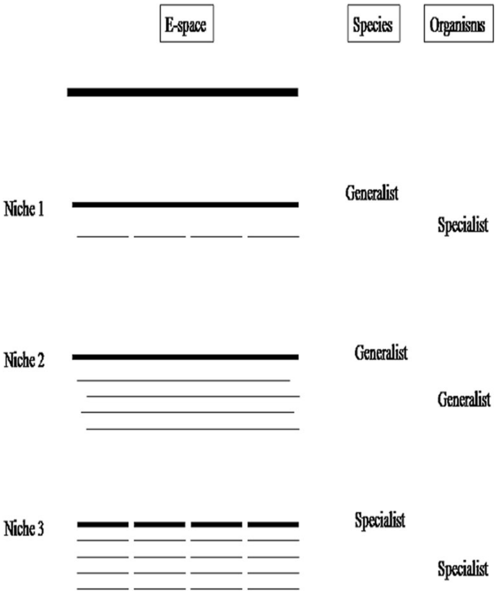

Fig. 1 Environmental space with niche breadth and value for each species and organism. Two types of species and organisms in terms of niche breadth: specialist or generalist. Note that each specialist species occupy a certain niche value, and their organisms occupy the same niche value. E space means environmental space

Premises

To understand which macroevolutionary process is more important on shaping diversification patterns, we assumed a spatially explicit model (Fig. 2; see all the premises in Table 1). Each geographic locality has a corresponding niche value (Birand et al. 2012); thus, each locality has a particular scenopoetic or bionomic value that organisms as well as species are adapted for. At the organismal level, evolutionary fitness is represented by reproduction and survival (Darwin 1859). We assumed panmictic species (i.e., random mate across organisms), where specialist as well as generalist organisms have the same probability to reproduce (Hubbell

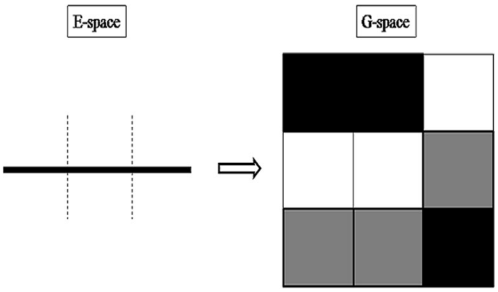

Fig. 2 Environmental space mapped into the geographic space. Environmental space is represented by a continuous variable, but we discretized it for the sake of simplicity. *Colors*: low (*white*), intermediate (*gray*), and high values (*black*). E space means environmental space, and G space means geographic space

Table 1 Premises to test predictions from both hypotheses: effect macroevolution or species selection

Features	Premises	References
Environmental space (E space)	Represented by scenopoetic and/or bionomic variables	Hutchinson (1978); Birand et al. (2012)
	Considered as a one-dimensional space	
Niche	Organismal and species trait (i.e., aggregate trait)	Vrba (1987)
	Heritable at both organismal and species level	
	Represents the breadth and value that each species and organism occupies in the environmental space	Quintero and Wiens (2013)
Geographic space	Spatial representation of the environmental space	Hutchinson (1957); Birand et al. (2012)
	Each geographic locality represents one value in environmental space	
Species and organisms	Three types of species and their organisms in terms of niche breadth:	
	Generalist species with generalist organisms (GEN-gen)	
	Generalist species with specialist organisms (GEN-spe)	
	Specialist species (SPE)	
Organismal-level processes	Three processes: reproduction, survival, and migration	Hubbell (2001)
	Reproduction is independent of niche	
	Fitness is assumed as survival	
	Survival is dependent on competition and niche value	Gascuel et al. (2015)
	For a given niche value, specialist organisms will present higher fitness than generalist organisms	
	Species fitness is modeled by a normal function	Wilson and Yoshimura (1994); Hubbell (2001)
	Migration is independent of niche	
	Probability to migrate between localities is modeled by an exponential function	Hubbell (2001)
Species-level processes	Two processes: speciation and extinction	Jablonski (2008); Mayr (1963); Gascuel et al. (2015); Ceballos and Erlich (2002); Reed (2005)
	Speciation is dependent on distance and time of isolation between populations and niche value of the locality where each population occurs	
	Extinction is dependent on geographical distribution and population size	
Effect macroevolution	GEN-gen and SPE species present higher diversification.	
Species selection	GEN-spe species presents higher diversification.	

2001). Probability to survive (hereafter, fitness) at a given locality is determined by competition and niche value (Gascuel et al. 2015). We assume that specialist organisms of specialist species are more adapted to their particular niche value than organisms of generalist species (Wilson and Yoshimura 1994; Burin et al. 2016). Thus, for a given niche value where specialist organisms are adapted for, they will be better competitors and, consequently, will present higher fitness than generalist organisms. Other factors could also determine how well adapted an organism is to a particular niche value (e.g., variation in physiological competences and generation duration), but, for the sake of simplicity, here we only assume the degree of specialization.

To model both factors—competition and niche value—determining organismal fitness, we assumed a normal fitness distribution of niche value for each type of species (Fig. 3). For specialist species, we assumed a normal distribution with a small standard deviation representing its specialization to a particular niche value (Fig. 3a). For generalist species, we assumed a normal distribution with larger standard deviation than for specialist species, but with a lower fitness peak (Wilson and Yoshimura 1994, Fig. 3b, c). Each type of organism also has its own normal fitness distribution, where specialist organisms have distributions with standard deviations similar to specialist species and generalist organisms have

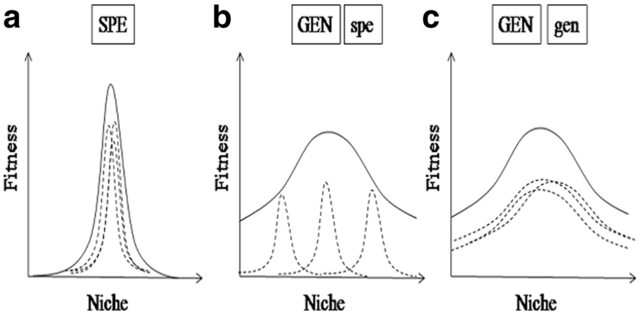

Fig. 3 Fitness distributions of niche value for three types of species. Species types are based on niche breadth: specialist species with specialist organisms (*SPE*), generalist species with specialist organisms (*GEN-spe*), and generalist species with generalist organisms (*GEN-gen*). *Thick lines* represent species distributions, whereas *dotted lines* represent distributions for organisms. Note that specialist species will have higher fitness than generalist species for the niche value where they are adapted for

distributions with standard deviations similar to generalist species. Specialist organisms of specialist species will have higher fitness for the niche value where they are adapted for than organisms of generalist species (Wilson and Yoshimura 1994).

The probability of organisms to disperse across geographic localities is independent of their niche characteristics (Hubbell 2001). Thus, we assumed that the probability to disperse is dependent on the distance between the localities where the organism occurs to the locality where the organism will disperse to ("isolation by distance" effect, Wright 1943). Therefore, the dispersion probability can be represented as an inverse exponential function of distance (Hubbell 2001).

At the species level, evolutionary fitness is represented by speciation and/or extinction (Jablonski 2008). We assumed the speciation events occurring in allopatry (Mayr 1963; Barraclough and Vogler 2000). Speciation is dependent on three main factors: distance between populations, time of isolation, and niche value (Mayr 1963; Gascuel et al. 2015). There is a minimum distance between populations where the probability to exchange organisms is so low that they can be considered isolated populations. Such probability of exchanging organisms between populations is determined by the exponential function aforementioned (Hubbell 2001). Speciation is also affected by the time when both populations have been isolated. In addition, populations may experience different selective regimes depending on the environment present at the geographic localities that they occupy. This environment is expressed by the niche value of each geographic locality (Gascuel et al. 2015, Fig. 2).

Two interrelated processes determine probability of extinction: geographical distribution and local population size (Ceballos and Erlich 2002; Reed 2005). Geographical distribution size represents the number of localities that the organisms of a given species occupy, and local population size is the number of organisms at a particular geographic locality. Each local population has a minimum size or threshold at which stochastic processes (demographic, environmental, or genetic) or inbreeding depression does not affect its persistence for a short time period (i.e., minimum viable population; Reed 2003). Thus, for a given species to go extinct, a gradual reduction of its geographical distribution is required until its last local population passes this threshold.

Predictions

Based on the multi-level hierarchical processes assumed as premises above, we derive several predictions of speciation for GEN-gen, GEN-spe, and SPE species (Table 2). First, we could expect that GEN-gen and GEN-spe species will have higher probability of speciation than SPE species (Gómez-Rodríguez et al. 2015). This would result because generalist species have more localities with suitable environmental conditions and/or biotic interactions than specialist species, resulting in larger geographic distributions (Slatyer et al. 2013). However, because populations of generalist species are evolutionary less fitted to a specific locality than populations of specialist species (Wilson and Yoshimura 1994, Fig. 3), thus more prone to local extinction, this might result in more isolated populations and consequently more speciation events. There are empirical evidences for this prediction for different groups such as amphibians (Gómez-Rodríguez et al. 2015) and vascular plants (Ozinga et al. 2013). Second, we could expect that SPE species will have higher

Table 2 Predictions for speciation and extinction for each type of species based on their niche breadth. *GEN-gen* generalist species with generalist organisms, *GEN-spe* generalist species with specialist organisms, *SPE* specialist species

	Predictions	Causes
Speciation	GEN-gen and GEN-spe > SPE	Generalist species have more localities with suitable niches, consequently higher geographical ranges. Thus, their populations are more likely to be isolated.
	GEN-gen and GEN-spe < SPE	Specialist species are more prone to present isolated populations because they have narrower niches, and, once a peripheral locality is colonized, there is a high probability of its population being isolated from the others.
Extinction	GEN-spe > GEN-gen > SPE	Competition is more important than niche breadth. Consequently, specialist species are better competitors within a given niche value than generalist species. Generalist species with generalist organisms have more availability of localities with suitable niches than specialist organisms.
	SPE > GEN-gen and GEN-spe	Niche breadth is more important than competition. Consequently, generalist species have more localities with suitable niches, higher geographic ranges, and number of populations.
	GEN-gen = GEN-spe = SPE	Migration and reproduction are more important than competition and niche value (at each locality).

probability of speciation than GEN-gen and GEN-spe species (Rolland and Salamin 2016; Burin et al. 2016). This would result because (i) populations of specialist species can colonize peripheral localities besides the fact that this will happen with low probability given that the dispersal process is modeled by an exponential function (Hubbell 2001); (ii) populations of specialist species will be evolutionarily more fitted for those peripheral localities than populations of generalist species (Wilson and Yoshimura 1994, Fig. 3); and (iii) peripheral populations are more likely to be isolated because the dispersal process is modeled by an exponential function, where distant localities have lesser probability of sharing organisms than nearby localities (isolation by distance effect, Wright 1943), and because they have narrower niches. As for the first prediction, there are also empirical evidences for this prediction for several vertebrate groups such as birds and mammals (Rolland and Salamin 2016; Burin et al. 2016).

Following the same premises, we also derive several predictions of extinction for GEN-gen, GEN-spe, and SPE species. First, we could expect that SPE species would have lower probability of extinction than GEN-gen and GEN-spe species (Rolland and Salamin 2016; Burin et al. 2016). This would result from specialist organisms of specialist species being better competitors than organisms of generalist species within a given locality, since the former organisms are better adapted to the available environmental conditions and/or biotic interactions (Wilson and Yoshimura 1994). Rolland and Salamin et al. (2016) showed that specialists are lesser prone to extinction than generalists for almost all amphibians, birds, and mammals. Moreover, we also expect that GEN-gen species would have lower probability of extinction than GEN-spe species. This could happen because even though generalist organisms will be evolutionarily less fitted to a particular locality than specialist organisms (Wilson and Yoshimura 1994), they will have the ability to occupy other localities to maintain viable populations (Fig. 3), a capacity that is not presented by specialist organisms of either generalist or specialist species. Our second prediction is that GEN-gen and GEN-spe species would have lower probability of extinction than SPE (Gómez-Rodríguez et al. 2015). This would result from generalist species having larger geographical distributions owing to their broader niches and, consequently, higher number of populations (Slatyer et al. 2013). Thuiller et al. (2005) showed that European plants with narrower niches present lesser probability of extinction than plants with wider niches. Third, we could expect that all three types of species will have the same probability of extinction (Birand et al. 2012). This would result from the interaction between migration and reproduction, which are niche-independent processes, overcoming the effects of competition and niche value at each geographic locality. We found no empirical but theoretical evidence for this prediction (Birand et al. 2012).

Assuming the balance between speciation and extinction, we should test these predictions to verify whether effect macroevolution or species selection is the main causal process shaping diversification patterns. According to our premises and predictions, if GEN-gen or SPE species present higher accumulation of species, then effect macroevolution can be considered the main causal process behind diversification given that the trait of interest is present at the organismal level (Vrba and Eldredge 1984). Otherwise, if GEN-spe species present higher accumulation of species, then species selection would be considered the main causal process given that the trait of interest is present at the species level and is different from the one present at the organismal level, thus causing a cross-level conflict (Diniz-Filho 2004; Jablonski 2008).

Moving forward

We consider our conceptual framework as a first formal attempt toward disentangling the macroevolutionary consequences of effect macroevolution and species selection. Indeed, our framework can guide future analyses explicitly aimed at evaluating whether effect macroevolution or species selection is more important to explain diversification patterns. To test our proposed predictions, we advocate the necessity to produce mechanistic models that, if possible, incorporate all aforementioned multi-level processes and are oriented by observed patterns (Grimm and Railsback 2005). A potentially fruitful research avenue is the development of individual-based models, where simulating the interaction of individuals at multiple levels can help understand the main processes shaping the properties of higher level patterns (DeAngelis and Mooij 2005; Grimm and Railsback 2005). Moreover, we also advocate that after answering the main question posed by our framework (effect macroevolution vs. species selection), other questions should be addressed. Among others, some relevant questions can be the following: Which causal processes are more important in a scenario with temporal variation in environmental conditions (see Gascuel et al. 2015)? What is the effect of neutral process—such as genetic drift, as the basis of broad-scale neutral dynamics—in diversification patterns (see Rosindell et al. 2015; Chevin 2016)?

Concluding remarks

Recently, several studies have highlighted the potential association between biological traits and diversification patterns. However, most of these studies are silent on how processes occurring at different biological levels could affect these patterns. Here, we have proposed a hierarchical conceptual framework to evaluate such multi-level processes and test for effect macroevolution and species selection driving macroevolutionary patterns. We considered the ecological niche as an appropriate biological trait that can undergo natural selection and highlighted the importance to define niche as an aggregate trait to help disentangle between macroevolutionary processes. Finally, we believe that mechanistic models can be a possible solution to understand the hierarchical nature of evolution.

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