

# Unifying macroecology and macroevolution to answer fundamental questions about biodiversity

30<sup>th</sup> Anniversary of Macroecology contribution at *Global Ecology and Biogeography*

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## Abstract

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The study of biodiversity started as a single unified field that spanned both ecology and evolution and both macro and micro phenomena. But over the 20<sup>th</sup> century major trends drove ecology and evolution apart and pushed an emphasis towards the micro perspective in both disciplines. Macroecology and macroevolution reemerged as self-consciously distinct fields in the 1970s and 1980s, but they remain largely separated from each other. Here we argue that despite the challenges it is worth working to combine macroecology and macroevolution. We present 25 fundamental questions about biodiversity that are really only answerable with a mixture of the views and tools of both macroecology and macroevolution.

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## Historical Context

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In Darwin's "On the Origin of Species" (1859), it is impossible to find a distinction between ecological and evolutionary processes; they were intertwined throughout. While several of Darwin's chapters were devoted to what we now perceive as purely evolutionary topics like transformations of species in the fossil record (Chapters 9 and 10) and hybridism (8), other chapters would be assigned to ecology such as the struggle for existence which involve reproduction and mortality (Chapter 4, Chapter 5). There are also several chapters addressing topics that are currently recognized as crossing both ecology and evolution (intraspecific variation – Chapters 1, 2 – and behavior – Chapter 7). Equally, Darwin made no distinction between micro and macro scales. He interwove the fossil record with agricultural breeding programs, and a local entangled bank of interacting species with the biogeographic distribution of organisms. Similar breadth can be seen in the writings of authors that pre-dated Darwin, such as von Humboldt (von Humboldt & Ross, 1852).

In the first half of the 20<sup>th</sup> century, a wedge began to form between the evolutionary and ecological sides of the field (Figure 1). On the one hand, ecologists became more interested in smaller scale phenomenon such as population dynamics and species interactions that could largely ignore evolutionary processes (Elton, 1927; Clements *et al.*, 1929). On the other hand, many evolutionary biologists, spurred on by linkages to genetics (Morgan & Biologiste, 1925) and the development of theoretical population genetics (Provine, 2001), shifted their focus to individual genes rather than whole phenotype. For example, the development of mathematical models that start with assumptions like "let the fitness of AA and Aa be 1 and of aa be 1-s" tend to underplay the ecological processes that lead to fitness differences that Darwin's writings so eloquently merged.

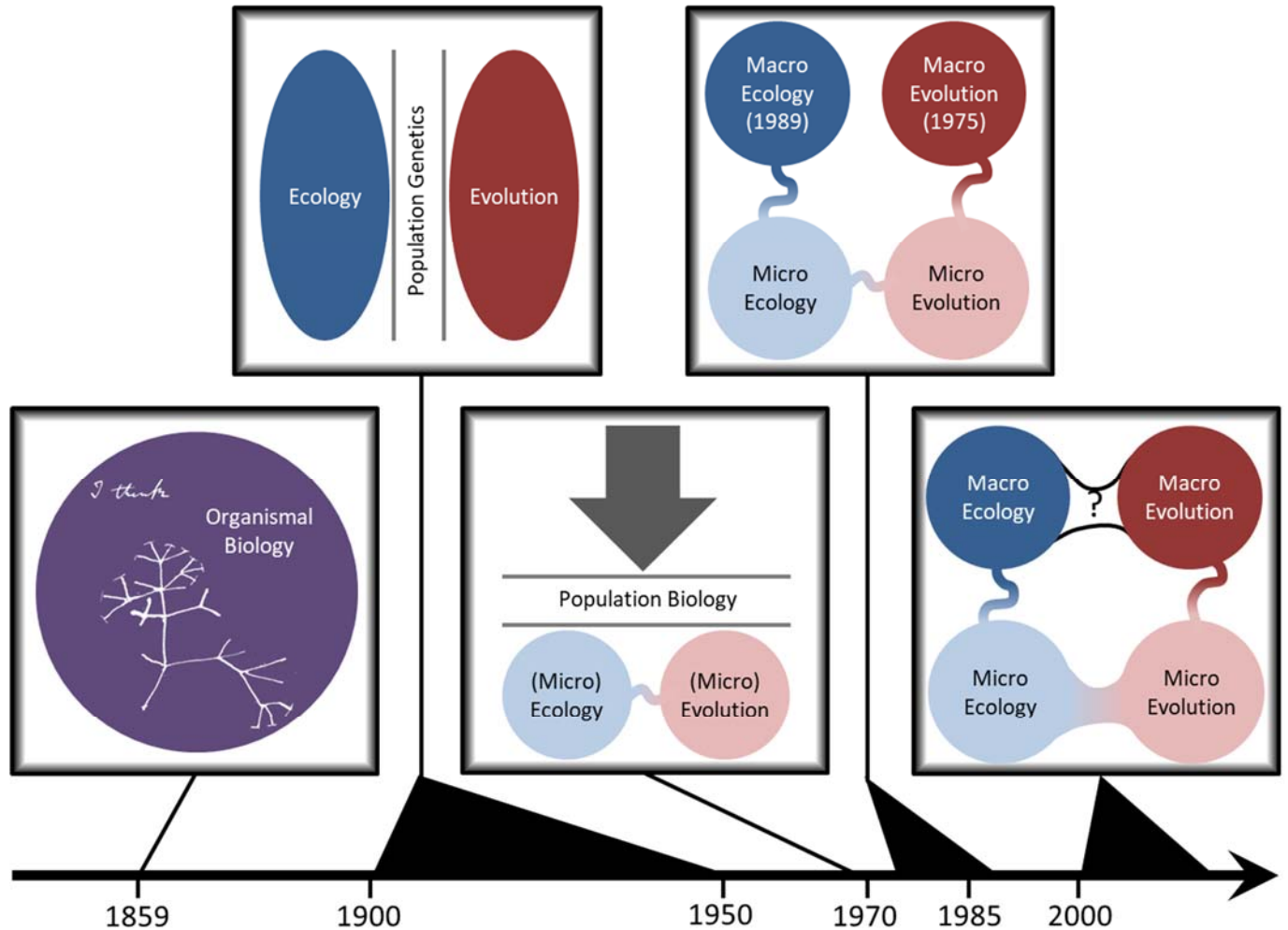
The latter half of the 20<sup>th</sup> century began to see the re-emergence of a connection. Some early descriptions of this can be seen in chapters of the edited volume "Evolution as a process" (Huxley *et al.* 1954) where evolutionary processes were said to lead to communities of interacting organisms (much like Darwin's entangled bank). Selection in natural environments began to be studied (Kettlewell, 1955; Ford, 1971). Likewise, the emergence of quantitative genetics (Crow & Kimura, 1970) and models of evolution of multivariate phenotypes (Lande, 1979) brought back a complex view of phenotype. From the ecology side, evolutionary ecology emerged as a field, inspired by Hutchinson's metaphor of the "ecological theater and the evolutionary play" (Hutchinson, 1965) and MacArthur and colleagues' models that looked at the evolution of ecologically relevant traits (MacArthur, 1961, 1962; MacArthur & Levins, 1964; MacArthur & Pianka, 1966).

102 The 1970s saw this reconnection of ecology and evolution develop more fully as part of  
the field of “population biology” – explaining ecological and evolutionary questions through basic  
105 population processes using simple differential equations involving birth, death, immigration and  
emigration, and speciation (Wilson & Bossert, 1971; MacArthur & Wilson, 1967; Levins, 1968).  
This population biology framing opened up new fields that combined evolutionary and ecological  
108 perspectives spanning a diverse array of questions including evolutionary ecology (Bulmer, 1994;  
Fox *et al.*, 2001), behavioral ecology (Alcock & Rubenstein, 1989) and life history theory  
(Stearns, 1976; Roff, 2002). The population biology approach has also seen a resurgence over the  
last decade under the label of “eco-evolutionary dynamics” which explores the evolutionary  
111 dynamics of traits that play out on the same time scales as ecological processes (Grant & Grant,  
1989; Yoshida *et al.*, 2003; Carroll *et al.*, 2007; Hendry, 2016; McPeck, 2017; Schoener,  
2011)(Metz *et al.*, 1996; McGill & Brown, 2007).

114 While the population biology research program succeeded in bringing ecology and  
evolution together in certain ways, it gave primacy to small-scale processes. This is essentially the  
philosophical notion of reductionism – explaining a system by breaking it into component parts  
and examining their interactions. This presumes the ability to scale up detailed models of  
117 population processes to answer macroevolutionary questions about species diversity and  
phenotype evolution or macroecological questions about the spatial variation in diversity and the  
relative abundance of species. While an active and interesting area of research, progress has been  
120 slow due to specific mathematical obstacles (O’Neill, 1979; McGill, 2019). The result is that  
embracing the population biology view, while helping to reunite aspects of ecology and evolution,  
drove a wedge between the micro- and macro-scale aspects of each discipline.

123 With micro-scale processes predominating in the population biology paradigm, this  
arguably diminished the importance and relevance of the macro-scale disciplines. As a result  
macroevolution and macroecology emerged as distinct, separately named fields (Stanley, 1975;  
126 Brown & Maurer, 1989). In evolution, the line is sharp and widely agreed upon – studies of  
processes within a species are microevolution, while macroevolution addresses questions above  
the species level (phylogenies, comparative evolution). In ecology, the line is blurrier.  
129 Microecology (more commonly just called ecology) studies small scales involving physiology,  
behavior, populations and communities; macroecology studies large spatial, temporal or  
taxonomic scales (Brown, 1995; Gaston and Blackburn 2000; McGill, 2019). Because both macro  
132 fields spent their first decades establishing themselves as independent fields, they have not looked  
externally often, leading to comparatively few links between macroecology and macroevolution.

135 To summarize (and admittedly oversimplify), the study of organismal biology started as a  
unified field, became for most practitioners split into distinct fields of ecology and evolution, then  
became further split into four fields with most practitioners focusing on micro vs macro versions  
of each field (Figure 1).



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144 *Figure 1 – A brief history of how Darwin's integrative vision of organismal biology became split*  
 147 *into first two and then four separate fields: microevolution, macroevolution, micro-ecology*  
 150 *(traditional population and community ecology), macroecology. In the bottom right panel, efforts*  
 153 *to link microevolution to macroevolution and micro-ecology to macroecology (narrow vertical*  
 156 *paths) are ongoing but difficult. Efforts to link microevolution and microecology (horizontal broad*  
 159 *connection) have been a major focus for recent decades. Efforts to link macroecology and*  
 162 *macroevolution (missing area shown by a question mark) have been, by comparison, much more*  
 165 *limited but are urgently needed.*

### Relationship of macroecology and macroevolution

153 Are we on our way to the seamless integration of ecology and evolution practiced by  
 156 Darwin? We would suggest not yet in an important way. The missing linkage in the history as  
 159 described above is a direct linkage between macroecology and macroevolution (question marks,  
 162 Figure 1), despite seeming a natural link given their strong match in embracing large scales.  
 165 Notably, the vertical linkages of the two macro-micro bridges have proven surprisingly resistant

159 to advances (notwithstanding some successes (Avise, 2000), and we suggest they will ultimately  
162 prove to be harder barriers to cross than the ecology-evolution divide (hence the thicker line in  
165 Figure 1) for some specific mathematical reasons (O'Neill, 1979; McGill, 2019). Regardless of  
168 one's view on the feasibility of spanning the macro/micro divide, the indirect, 3-legged route of  
171 linking macroevolution to microevolution to microecology to macroecology is hopelessly  
174 unwieldy. **The main thesis of this paper is that organismal biology is missing - and badly  
177 needs - a re-unification directly between macroecology and macroevolution.**

180 A very simple examination of the limited interactions between macroecology and  
183 macroevolution can be done using bibliometric analysis, albeit in a necessarily quite simplistic  
fashion. In particular many macroecological and macroevolutionary papers often do not use those  
keywords (and necessarily couldn't before the words were coined), so this analysis clearly omits  
relevant papers, but we believe it to be a sample that is not biased. An analysis of words found in  
keywords and abstracts using Web of Science was performed in March 2018. A search for  
derivatives of macroecology ("macroecolog\*") found 1,814 papers going back to the coining of  
the term in 1989 (Brown & Maurer, 1989) and roughly about 150 papers/year in recent years.  
Derivatives of macroevolution ("macroevolution\*") found 2,570 papers going back to Stanley's  
1975 coining of the term (Stanley, 1975) with about 220 papers/year in recent years. Although,  
again, by no means does this approach capture all macroecological or macroevolutionary papers,  
these results suggest that a substantial sample is obtained in searches using these keywords. This  
analysis supports the notion that both of the macro fields are growing rapidly since their relatively  
recent launches. It also supports the notion that macroecology and macroevolution are infrequently  
practiced as overlapping fields. Only 105 papers starting in 2000 (about 10 papers/year) contain  
both macroecology and macroevolution (macroecolog\* and macroevolution\*). By this method,  
only 4-6% of the papers that are explicitly macroecological or macroevolutionary recognize  
themselves as interdisciplinary between both fields. This crude analysis suggests that while  
linkages between macroecology and macroevolution do exist they are not yet common. In  
recognition of the existence of some links between macroecology and macroevolution, Box 1 gives  
some well-known examples of linkages between both disciplines.

### Box 1: Examples of prominent existing work linking macroecology and macroevolution

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Despite our thesis that macroecology and macroevolution tend to have distinct boundaries, there are some exemplary cases where the connections are strong. The following demonstrate and acknowledge that some work uniting these fields has been done, and highlights the importance of making these connections.

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● Biogeography and paleontology (and paleoecology) are long-standing fields that integrate ecology and evolution at macro scales. Paleontology is full of examples such as the study of how extinction rates depend on body size (e.g. Jablonski & Raup, 1995) or how phenotype changes through time (e.g. Foote, 1997) or range shifts due to climate (Lyons, 2003) or ecological processes in fossil communities (Blois *et al.*, 2014).

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● MacArthur was key in re-introducing evolutionary thinking into ecology (MacArthur, 1961). Examples that are more macro in nature include the idea of limiting similarity (MacArthur & Levins, 1967), his exploration of the causes of the latitudinal gradient in richness (MacArthur, 1969), his work on R vs K selection (MacArthur, 1962), or even his explicit recognition of the importance of evolutionary processes in the Theory of Island Biogeography (Chapter 7 in MacArthur & Wilson, 1967).

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● The exploration of adaptive radiations on island-like systems has long necessitated combining macroecology and macroevolution (Grant & Grant, 1989; Schluter, 2000). The study of ecological morphotypes and their evolution across multiple islands is a related example (Gillespie, 2004; Losos, 2011)

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● Ecological neutral theory with speciation (Hubbell, 2001) clearly links the two fields. More generally, with growing recognition of the importance of the regional pool of species for ecology (Ricklefs & Schluter, 1993b), there has been increased interest in exploring the macroevolution of regional pools of species which then constrain local community assembly (Mittelbach & Schemske, 2015; Ricklefs, 2015). Also related are studies comparing the assembly of communities through colonization vs. speciation (Rummel & Roughgarden, 1985).

● Similarly, phylogenetic community ecology has sought to understand how the macroevolutionary history of the regional pool interacts with ecological and biogeographic processes to produce observed assemblages of co-occurring taxa (Webb *et al.*, 2002; Emerson & Gillespie, 2008; Cavender-Bares *et al.*, 2009)

● Niche conservatism is explicitly an evolutionary hypothesis about an ecological concept (that niches evolve slowly and thus show conservatism over a phylogeny) (Peterson *et al.* 1991, Ackerly 2003, Wiens & Graham 2005)

● Ricklefs's study of taxon cycles on islands (Ricklefs & Cox, 1972), the role of distinct macroevolution on different continents in species richness (Latham & Ricklefs, 1993), and numerous papers at the interface of niche, community and macroevolution (Cox & Ricklefs, 1977; Ricklefs, 2010, 2011) and multiple calls for the importance of merging ecological and evolutionary thinking (Ricklefs & Schluter, 1993a; Ricklefs, 2007)

● Rosenzweig's examination of competitive speciation (ecological conditions leading to sympatric speciation; Rosenzweig, 1978) and the study of incumbent replacement (increased diversification rates after competitors go extinct; Rosenzweig & McCord, 1991) are also examples.



234 There are good reasons for this disconnect between the two macro fields. As noted, both  
fields are relatively new, placing an emphasis on self definition rather than reaching out to other  
237 fields. Additionally, the two fields operationalize and measure their variables differently even  
though they speak of the same concepts (Table 1). This is in part because the sources of the data  
240 are distinct and in part because the perspectives and priorities are distinct. Macroevolutionists  
focus on changes through time and thus use either stratified fossils or phylogenies derived from  
current molecular sequences or both. Macroecologists focus on space and thus use biological  
inventories in the present day. Clearly both of these perspectives are crucial understanding  
diversity in space and time, but integrating these perspectives presents challenges.

243 The key variable that both fields share is an interest in species richness, although  
macroevolution initially sees this as an outcome of speciation and extinction through time, while  
macroecology initially sees this as an ecological outcome of dispersal and of past and present  
246 climatic conditions (Belyea & Lancaster, 1999) varying across space at one point in time (but as  
this paper highlights, ecological conditions and diversification are not independent of each other,  
also see Ricklefs & Schluter, 1993). Moreover, macroevolution tends to focus on richness of a  
249 monophyletic group of species (e.g., a specific clade of frogs), whereas macroecology tends to  
focus on richness of an assemblage (e.g., all trees) that can be quite polyphyletic.

Such differences extend to other variables of interest as well. Both areas focus on  
phenotype. Macroecologists can focus on a complex multivariate set of features but are limited to  
252 a point in time. Macroevolutionists bring a temporal perspective but are limited to a simpler view  
of phenotype due to the limitations of fossils and phylogenetic methods. Likewise, both fields  
focus on abundance and distribution. But abundance is not estimatable in phylogenies and spottily  
255 preserved in the fossil record and distributions can only be approximated from fossil and  
phylogenetic inference, leading to a very coarse view of historical distribution. Macroecologists  
can measure these with much more precision at fine grained spatial scales, but fail to see abundance  
258 and distribution as dynamic and changing through evolutionary time. Finally, both fields have  
notions of colonization, but macroevolution looks at rare vicariance or founder events across  
biogeographic provinces while macroecology looks more at the scale of metapopulation dynamics.

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	<b>Macroecology</b>	<b>Macroevolution</b>
Diversity	Richness, evenness, abundance (often of polyphyletic groups)	Richness (typically within a monophyletic clade)
Traits	Morphospace, trait volumes and niches across an assemblage, functional diversity	Evolution of morphospace, trait volumes and niches across a phylogeny
Diversification	Phylogenetic diversity indices	Speciation, extinction, diversification rates
Distribution	Range size, habitat preferences	Biogeographic province
Species interactions (e.g. competition, predation, parasitism)	Interaction webs	Coevolution
Abiotic environment	Climate variation across space, static view of soils/topography	Climate variation across time, Geologic change in topography

267 *Table 1 – Comparison of macroecological vs. macroevolutionary views of different variables*

270 As just shown, the overlap in concepts of interest to both macroecology and  
 273 macroevolution hides deeper divides. Methodological challenges exist due to their disparate data  
 276 sources. But more fundamentally, there is a key conceptual difference as well. Macroevolution  
 tends to focus on temporal processes and macroecology tends to focus on spatial processes. Core  
 questions in macroevolution have a tendency to center on questions of rates (speciation, extinction  
 and net diversification) and how these rates change through time within and across clades. Core  
 questions in macroecology tend to center on levels (not rates) like abundance, richness, range size,  
 and traits and how these levels change across space and across taxa.

### **Reasons why a unification is needed**

279 Scientific inquiry does not arbitrarily divide itself into spatial questions vs. temporal  
 282 questions. Nor does scientific inquiry limit itself to a single source of data at a time. These are  
 285 human created barriers. Although there may have been pragmatic reasons (including social and  
 288 computational limits) that have slowed the cooperation of macroecology and macroevolution, the  
 conceptual barriers are readily overcome. Indeed, although we have emphasized the differences  
 and challenges thus far, the overlap in topics of interest between macroecology and  
 macroevolution is striking (Table 1). To the degree that large spatial processes play out across long  
 temporal time scales and vice versa (Stommel, 1963; Wiens, 1989; Levin, 1992), macroecology  
 and macroevolution will also naturally look towards each other rather than towards the “micro”  
 versions of their fields. In fact, we suggest macroecology and macroevolution urgently need to  
 cooperate because there are obvious and important questions that combine macroecological and  
 macroevolutionary variables and perspectives. Figure 2 gives a conceptual framework that  
 suggests many overlapping questions, 25 of which are then listed in more detail in Table 2. All of

291 these questions are “big” questions in the sense that they have long been speculated about, in some  
cases for over 100 years. For example, the question “are closely related species likely to have  
294 similar niches and compete more intensely with each other?” (Question #15 in Table 2) was  
hypothesized by Darwin (1859). All of the listed questions remain largely unanswered (but see  
Box 1) because scientists have not yet methodologically bridged the divide between macroecology  
297 and macroevolution. Note that the structure of Figure 2 naturally divides the questions into three  
categories: where causality flows from ecology to evolution, where causality flows from evolution  
to ecology, and cross-cutting questions where the flow of causality is bidirectional or complex,  
and Table 2 is organized accordingly. In the next section we give some case studies of a subset of  
300 the questions to provide more depth.

How does factor in Row		Affect factor in Column							
		Abundance	Interaction	Trait	Niche	Dispersal	Diversity	Diversification	Phyl. relatedness
Ecology	Abundance	<b>Traditional Macroecology</b>						1 <sup>A</sup> ,4	
	Interaction						1 <sup>A</sup> ,25	8	
	Trait						1 <sup>A</sup> ,21		
	Niche						24	9	
	Dispersal						5,6		
	Area						3		
	Isolation						3	9	
	Topography						2 <sup>B</sup> ,21	9	
Evolution Both	Climate						7,21		
	Taxonomic group	10 <sup>C</sup>							
	Diversity					18 <sup>E</sup>	19 <sup>F</sup> ,22	22	
	Diversification	10 <sup>C</sup>	14,25	23,24	13	20	<b>Traditional Macro-evolution</b>		
	Phyl. relatedness	10 <sup>C</sup>	11 <sup>D</sup>	15	15	18 <sup>E</sup>			
Evolution	Geological time	12	16	17	17	19 <sup>F</sup>			

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306 *Figure 2: The relationships between macroecology and macroevolution. The rows contain possible explanatory variables (labelled and categorised at the left). The columns contain possible dependent variables (labelled and categorised at the top). Some of these variables are ecological (in blue), and some of these variables are evolutionary (in red). Diversity and taxonomic group are shared between ecology and evolution (in purple). Abiotic variables are shown in italics, while biotic variables are shown in bold. Each intersection or grid cell is a potential question of the form “how does X affect Y?”. Historically, macroecology predominantly focused on intersections of variables that were ecological, while macroevolution focused on variables that were evolutionary, although this division has never been absolute (Box 1). Questions involving ecological variables impacting evolutionary variables and vice versa (light purple regions) represent the emerging synthesis between macroecology and macroevolution as argued for here. The fact that diversity and the importance of distinct taxonomic groups is shared between macroecology and macroevolution creates a boundary region (dark purple). Note that “diversity” appears as a single factor in the diagram, but could refer to taxonomic, functional or phylogenetic diversity and could equally refer to alpha, beta, or gamma diversity. Numbers in the grid cells represent questions which are listed in Table 2. Bold numbers represent case studies which are expanded upon in this paper and their superscript letter indicates which case study (A-F) they refer to. Abiotic variables affecting abiotic variables are earth science questions and not included here. One can place allied fields like biogeography as a stripe spanning the abiotic variables running across the width of the diagram and paleontology across the bottom row. This placement shows that there is clearly overlap, but these fields do not cover the full range of what we propose here.*

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<b>Ecological factors affecting evolution</b>	
<b>1</b>	<b>What ecological conditions enable radiations? (case study A)</b>
<b>2</b>	<b>How do diversification rates scale with topography? (case study B)</b>
3	How does area and isolation influence relative importance of speciation and colonization?
4	Do diversification rates vary with commonness and rarity?
5	How do dispersal affect diversification?
6	Does spatial sorting lead to speciation of good dispersers more than poor dispersers?
7	How does environment and environmental change affect diversification rates?
8	Do tightly coupled biotic interactions leading to co-evolution reflect as parallel phylogenies in the interacting taxa?
9	Does evolution into new habitats occur faster or slower than vicariance events between islands?
<b>Evolutionary factors affecting ecology</b>	
<b>10</b>	<b>How do relative abundance patterns respond to macroevolution? (case study C)</b>
<b>11</b>	<b>Are ecological interactions determined by shared evolutionary history? (case study D)</b>
12	How does relative abundance persist or change through geological time and across the tree of life?
13	How does dispersal ability evolve and change?
14	How does diversification affect the number of interactions per species?
15	Are closely related species more likely to be similar in phenotype and niche?
16	Over what time scales do species interactions remain strong?
17	Are niches and phenotypes static? Or if they change over time do they change in a directional, random or other systematic fashion?
<b>Cross cutting questions</b>	
<b>18</b>	<b>What is the role of evolution in invasion? (case study E)</b>
<b>19</b>	<b>Does diversity saturate in space and/or time? (case study F)</b>
20	How do the relative rates of colonization vs. speciation influence alpha, beta and gamma taxonomic, functional and phylogenetic diversity?
21	What is the relative importance of environmental heterogeneity and biotic heterogeneity in speciation rates?
22	Does diversity beget diversity?
23	How do the relative rates of colonization vs speciation influence niche packing and filling?

24	Does speciation create niches or does empty niche space drive speciation?
25	What is the interplay between diversification and coexistence mechanisms?

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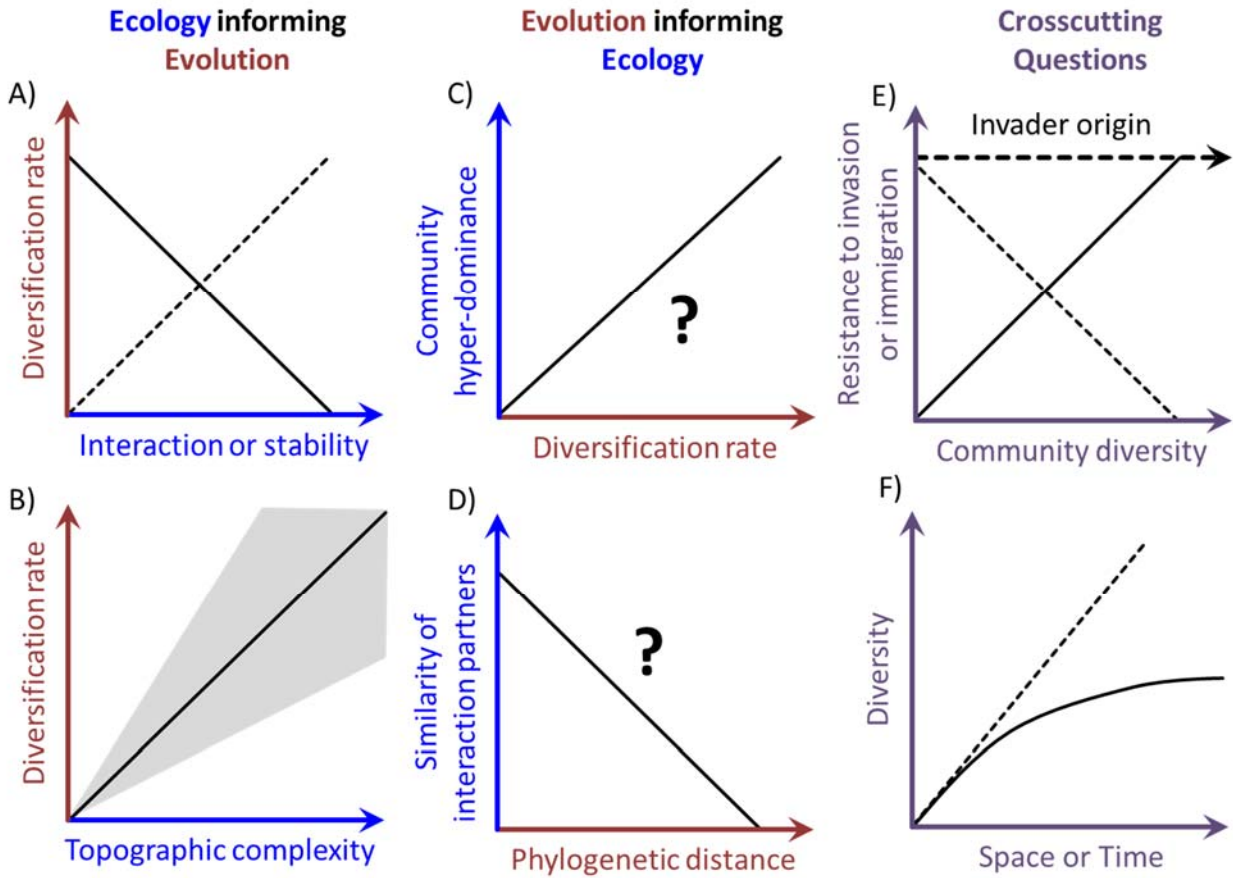
*Table 2 – A list of 25 important questions at the interface between macroecology and macroevolution. Bolded questions are case studies that are each expanded on below. Cross-cutting questions involve diversity which is the one variable currently shared between macroecology and macroevolution. The sEcoEvo working group generated this list of questions during a working group at sDiv.*

342 It is beyond the scope of this paper to review existing literature and highlight the key paths  
forward to all 25 questions listed in Table 2 (and the countless others that we have not identified,  
but are equally important). However, to provide some depth and make our claim of importance for  
these mostly unanswered questions more concrete, we highlight six of these questions (in bold in  
Figure 2 and Table 2, also see Figure 3) and briefly address them as case studies.

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**Case study A (Question 1, Figure 3a): What ecological conditions enable radiations?**

348 What ecological conditions promote or inhibit evolutionary diversification? Adaptive  
radiations occur when a clade rapidly speciates and diversifies into many novel niches, often in  
response to ecological opportunities (Schluter, 2000). The existence of dramatically speciose  
adaptive radiations begs the question of what properties of systems where these radiations occur  
351 promote such diversification? Conversely, are systems with low species richness, often in harsh  
temperate areas and characterized by a few representatives of distantly related clades, limited by  
dispersal over geologic timescales or is the evolution of novel forms in such low richness systems  
354 limited by some property of these systems? One long-standing hypothesis for adaptive radiations  
is that the ecology of insular systems is defined by release of populations from their ancestral  
predators, parasites, and/or competitors (Schluter, 2000; Mahler *et al.*, 2010; Losos 2010; Stroud  
357 & Losos 2016). Conversely, increased diversity in the tropics has been attributed to increased, not  
decreased, interaction intensity between an increased number of interactors (Gillespie, 2004; Nosil  
& Crespi, 2006). Clearly ecological drivers of evolutionary radiation exist, but which direction  
360 those drivers point (from increased interaction to diversity, or from decreased interaction to  
diversity) remains unresolved. An alternative but complementary perspective posits that  
ecological stability can either promote or inhibit diversification. If the tropics have maintained  
363 stable abiotic conditions, this may facilitate consistent accumulation of species (Pianka, 1966; Jetz  
& Fine, 2012). By the same argument, temperate areas, with frequent glacial/interglacial  
disturbance, inhibit diversification. In contrast, it has been recently hypothesized (Rominger *et al.*,  
366 2017) that the non-equilibrium dynamics of ecosystems could open opportunity for evolutionary  
radiations to permit the system's relaxation back to ecological equilibrium. If insular systems  
quickly lose their isolation (e.g. through human introduction of new species) then relaxation could  
369 instead be achieved by invasion (Helmus *et al.*, 2014). This could help explain both the incredible  
adaptive radiations on islands, but also the dramatic prevalence of invasive species.



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375 *Figure 3. Hypothetical relationships between driver and response variables for six case studies*  
 378 *taken from Table 2. The first column represents case studies A and B where ecological factors*  
*primarily influence evolutionary patterns and processes. The second column represents case*  
*studies C and D where evolutionary factors primarily influence ecological process/pattern. The*  
*third column represents cross-cutting case studies E and F that address ecological and*  
*evolutionary processes and feedbacks.*



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**Case Study B (Question 2, Figure 3b): How do diversification rates scale with topography?**

384 Topographic complexity (ruggedness and elevational range) has long been linked to high  
standing diversity and to processes of speciation. For example, the Andes mountains are home to  
the highest diversity in South America for both birds (Rahbek & Graves, 2001) and plants (Mutke  
*et al.*, 2011), and a lupine clade in the Andes has speciated at rates approaching those of classic  
387 island radiations (Hughes & Eastwood, 2006). The geologic processes generating oceanic islands  
similarly create diverse and isolated habitats, long hypothesized to contribute to dramatic  
radiations (Wilson, 1961; Ricklefs & Cox, 1972), as do isolated continental mountain tops (sky  
390 islands)(McCormack *et al.*, 2009). What ecological processes interact with topographic  
complexity to ultimately lead to changed diversification rates? Topographic complexity interacts  
with two ecological properties of species (dispersal ability and tolerance or niche breadth) to  
393 influence evolutionary processes. Specifically, more topographic complexity and shorter dispersal  
and narrower tolerances increase the possibility of local adaptation, genetic isolation and ensuing  
allopatric speciation processes. The interactions between mountains and changing climate (such  
396 as the Plio-Pleistocene glacial-interglacials) can add to the environmental heterogeneity and local  
adaptation increasing speciation (McCormack *et al.*, 2008; Rangel *et al.*, 2018) but simultaneously  
make it easier to track climate with short range dispersal decreasing extinction risk (Colwell *et al.*,  
399 2008).

402 **Case study C (Question 10, Figure 3c): How do relative abundance patterns respond to  
macroevolution?**

Do the diversification processes that produce a set of species influence the relative  
abundances (species abundance distribution or SAD) of those species? There are several  
405 developing lines of evidence that suggest high levels of diversification lead to more uneven SADs  
with a few hyperdominant species and many very rare species. The highly diverse Amazon  
rainforest shows extreme hyperdominance: 1.4% of tree species in the Amazon account for half of  
408 all individuals, whereas most remaining species are extremely rare (Ter Steege *et al.*, 2013; Slik  
*et al.*, 2015) and on a 50 ha plot on Barro Colorado Island 2.9% of species make up approximately  
half of all individuals. SADs also seem to change shape with greater time available for  
411 macroevolution (Craven *et al.*, 2019). Proportionately more rare species tend to be in more  
speciose genera and families (Harte *et al.*, 2015). The exact processes by which this evolutionary  
outcome (high standing species diversity) translates to this particular form of species abundance  
414 distribution is an open question. One possibility is that food-web theory predicts that higher  
dominance is expected to result in more stable communities (Emmerson & Yearsley, 2004).  
Conversely abundance could affect speciation rates (Makarieva & Gorshkov, 2004). But how all  
417 of these ecological factors cause, or are caused by, the evolutionary processes leading to high  
diversity remains an open question.

420 **Case study D (Question 11, Figure 3d): Are ecological interactions determined by shared  
evolutionary history?**

The relatively high level of specialization observed in host-parasite and plant-herbivore  
423 interaction networks begs the following question: at macroecological scales, are ecological  
interactions constrained primarily by their (co)evolutionary history or by their ecological distance  
(i.e., a combination of geographical ranges and preferred environmental conditions)? Considering  
426 host parasite interactions in particular, on the one hand, there is evidence that differences in

429 parasite communities associated with different host species are driven by environmental  
dissimilarity and phylogenetic distances among hosts, but not by geographical distance (Krasnov  
*et al.*, 2010). This finding has been interpreted as evidence of environmental filtering acting on the  
community of parasites at the “macro” scale (Krasnov *et al.*, 2014). On the other hand, there is  
432 evidence that differences in parasite communities across hosts are driven by parasite geographic  
ranges and not phylogenetic distance, despite a strong apparent signal of phylogenetic  
conservatism (Calatayud *et al.*, 2016; also see similar results in insect-host associations (Nylin *et al.*,  
2018)). The field of community phylogenetics also touches on interactions between species  
435 based on the amount of their shared evolutionary history (Webb *et al.*, 2002; Cavender-Bares *et al.*,  
2004; but see cautions in Mayfield & Levine, 2010). This case study is a good example of the  
interrelationships among the questions. Question 11 frames this as evolution driving ecology, but  
438 Question 8 is qualitatively the same question with ecology driving evolution.

### 441 **Case Study E (Question 18, Figure 3e): What is the role of evolution in invasion?**

441 Invasive species are a major component of global change (Millenium Ecosystem  
Assessment, 2005). Invasion is largely perceived as a solely ecological process despite  
evolutionary studies (Roderick & Navajas, 2003). But there are multiple ways in which invasion  
444 and evolution interact (Vermeij, 1996; Pantel *et al.*, 2017) including, before, during and after the  
invasion event. Focusing on evolution of a community before it is invaded, note that invasion  
and speciation are the primary alternatives for new species to contribute to faunal buildup and  
447 assembly. To what degree does having a community primarily derived from invasion differ from  
a community primarily derived from speciation? Rummel and Rougharden (1983, 1985) suggest  
that invasion-structured communities are more tightly packed in niche space but less stable and  
450 more open to invasion. In contrast, the invasion/evolution-in-place distinction has been one of  
the main arguments in support of the notion that remote islands (with biota assembly primarily  
driven by speciation) are more susceptible to invasion, although tests of high island invasibility  
453 suggest that it may be restricted to tropical islands (Turbelin *et al.*, 2017). Looking at the role of  
evolution during invasion, many have noted that the degree of fit of the invading species into the  
established morphospace (Moulton & Pimm, 1983), the phylogenetic position of the invader  
456 relative to species it will interact with (Pearse & Altermatt, 2013), and the phylogenetic clade  
(Binggeli, 1996) can all be predictive of invasion success. And there are interesting questions of  
evolutionary response of the invader and the invaded community after an invasion event. For  
459 example it has been suggested that invasive species may be freed from their predators and  
parasites (the ‘enemy release’ hypothesis; Keane & Crawley, 2002) leading to potential  
evolutionary opportunities including the possibility of “Evolution of Increased Competitive  
462 Ability” or EICA (Blossey & Notzold, 1995) although evidence is not conclusive (Willis *et al.*,  
2000). The act of being invasive may also select for individuals that are successful invaders  
including increased dispersal ability (Phillips *et al.*, 2006) or the notion that selection during an  
465 invasion may be spatially structured (e.g. different at the invasion front) (Shine *et al.*, 2011) or  
admixtures (geographic hybrids)(Kreherwinkel & Tautz, 2013). The species in the invaded  
community may also show an evolutionary response to the invader (Goergen *et al.*, 2011) or  
468 exploit an invader as a resource (Carroll *et al.*, 2005). Many of these questions are also highly  
relevant as climate change rearranges species that co-occur and leads to non-analogue  
communities.

### 471 **Case Study F (Question 19, Figure 3f): Does diversity saturate in space and/or time?**

Both macroecology and macroevolution ask the question of whether or not there is an upper limit to diversity. Macroecologists tend to focus on spatial patterns as an indicator of saturation (Figure 3e). One classic approach has been to ask how the size of the regional species pool influences diversity at local scales (Ricklefs, 1987; Pärtel *et al.*, 1996; Cornell & Harrison, 2014; Harmon & Harrison, 2015; Mittelbach & Schemske, 2015; Alroy, 2018). By contrast, macroevolutionary studies tend to focus on saturation of diversity through time (Phillimore & Price, 2008; Etienne & Haegeman, 2012; Moen & Morlon, 2014). In this context, saturation is revealed by a plateau of diversity over long time scales (Sepkoski, 1978; Rabosky & Lovette, 2008; Rabosky, 2013), although a plateau could also just indicate an equilibrium of speciation and extinction rates not caused by saturation (Wagner *et al.*, 2014). A unified approach to saturation over space and time will require the full integration of both ecological and evolutionary perspectives. Perhaps, for example, local communities can be saturated over short time scales, but such saturation breaks down over long time scales, as evolution of novel traits and lifestyles allow coexistence when none was possible before. We suggest that future studies consider saturation from both temporal and spatial perspectives, unifying macroecological and macroevolutionary approaches to this critical question. Two recent papers, a simulation (Herrera-Alsina *et al.*, 2018) and an empirical study of the fossil record (Close *et al.*, 2019), suggest that ecological processes at local scales may constrain macroevolutionary processes of diversification and macroecological factors like species range sizes taking place out over large spatial and long temporal scales.

## 492 **Conclusions**

The modern push to reconnect ecology to evolution (Hendry, 2016; McPeck, 2017) is occurring predominantly at micro-scales, connecting microevolution (e.g. intraspecific phenotypic evolution) with microecology (e.g. predator-prey species interactions). Darwin would never have attempted to understand one without the other. Yet macroecology and macroevolution have developed largely independently (but see Box 1) since their conceptualization (1975 and 1989 respectively). Because the roots of the two fields have been so distinct in data and questions (Figure 2, Table 1), the fields have largely functioned independently. However, as we have argued (Figure 3, Table 2), many of the most interesting and important questions span both fields and will require synthesizing the data, tools and perspectives of the two research fields to proceed. We see signs of this happening. The British Ecological Society Special Interest Group on Macroecology openly encourages participation by, and contributions from, both macroecology and macroevolution, as does this journal. We hope this concept piece will further encourage this much needed unification.

## 507 **Acknowledgements**

This paper is a joint effort of the working group sEcoEvo kindly supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118). Brian McGill acknowledges USDA Hatch grant to MAFES #1011538 and NSF ABI grant #1660000.

- Ackerly, D. D. (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164(S3): S165-S184.
- Alcock, J. & Rubenstein, D.R. (1989) *Animal behavior*. Sinauer Associates Sunderland, MA, USA.
- Allesina, S. & Tang, S. (2012) Stability criteria for complex ecosystems. *Nature*, **483**, 205.
- Alroy, J. (2018) Limits to species richness in terrestrial communities. *Ecology letters*, 21, 1781-1789.
- Avise, J.C. (2000) *Phylogeography: the history and formation of species*. Harvard university press.
- Belyea, L.R. & Lancaster, J. (1999) Assembly rules within a contingent ecology. *Oikos*, 402-416.
- Binggeli, P. (1996) A taxonomic, biogeographical and ecological overview of invasive woody plants. *Journal of vegetation Science*, **7**, 121-124.
- Blois, J.L., Gotelli, N.J., Behrensmeier, A.K., Faith, J.T., Lyons, S.K., Williams, J.W., . . . Eronen, J.T. (2014) A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen associations across the late Quaternary. *Ecography*, 37, 1095-1108.
- Blossey, B. & Notzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887-889.
- Borda-de-Água, L., Whittaker, R.J., Cardoso, P., Rigal, F., Santos, A.M., Amorim, I.R., . . . Borges, P.A.V. (2017) Dispersal ability determines the scaling properties of species abundance distributions: a case study using arthropods from the Azores. *Scientific reports*, **7**, 3899.
- Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243**, 1145-1150.
- Brown, J.H. (1995) *Macroecology*. Univ of Chicago Press, Chicago.
- Brown, J.H. (2014) Why are there so many species in the tropics? *Journal of biogeography*, **41**, 8-22.
- Bulmer, M. (1994) *Theoretical evolutionary ecology*. Sinauer Associates, Sunderland, MA.
- Calatayud, J., Hórreo, J.L., Madrigal-González, J., Migeon, A., Rodríguez, M.Á., Magalhães, S. & Hortal, J. (2016) Geography and major host evolutionary transitions shape the resource use of plant parasites. *Proceedings of the National Academy of Sciences*, **113**, 9840-9845.
- Carroll, S.P., Hendry, A.P., Reznick, D.N. & Fox, C.W. (2007) Evolution on ecological time-scales. *Functional Ecology*, **21**, 387-393.
- Carroll, S.P., Loye, J.E., Dingle, H., Mathieson, M., Famula, T.R. & Zalucki, M.P. (2005) And the beak shall inherit—evolution in response to invasion. *Ecology Letters*, **8**, 944-951.
- Cavender-Bares, J., Ackerly, D., Baum, D. & Bazzaz, F. (2004) Phylogenetic overdispersion in Floridian oak communities. *The American Naturalist*, 163, 823-843.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology letters*, 12, 693-715.
- Clements, F.E., Weaver, J.E. & Hanson, H.C. (1929) *Plant Competition: an Analysis of Community Functions*. Carnegie Institute of Washington, Washington DC.

- 558 Close, R., Benson, R., Alroy, J., Behrensmeyer, A., Benito, J., Carrano, M., . . . Uhen, M. (2019)  
Diversity dynamics of Phanerozoic terrestrial tetrapods at the local-community scale.  
*Nature Ecology and Evolution*,
- 561 Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C. & Longino, J.T. (2008) Global  
warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *science*,  
**322**, 258-261.
- 564 Cornell, H.V. & Harrison, S.P. (2014) What are species pools and when are they important?  
Annual Review of Ecology, Evolution, and Systematics, 45, 45-67.
- 567 Cornell, H.V. & Lawton, J.H. (1992) Species Interactions, Local And Regional Processes, And  
Limits To The Richness Of Ecological Communities - A Theoretical Perspective. *Journal  
Of Animal Ecology*, **61**, 1-12.
- 570 Cox, G.W. & Ricklefs, R.E. (1977) Species diversity and ecological release in Caribbean land  
bird faunas. *Oikos*, 113-122.
- 573 Craven, D., Knight, T.M., Barton, K.E., Bialic-Murphy, L. & Chase, J.M. (2019) Dissecting  
macroecological and macroevolutionary patterns of forest biodiversity across the  
Hawaiian archipelago. *Proceedings of the National Academy of Sciences*, 201901954.
- Crow, J.F. & Kimura, M. (1970) *An Introduction to Population Genetics Theory*. Harper & Row,  
New York.
- 576 Darwin, C. (1859) *On the origin of species*. Clows and Sons, London.
- Elton, C. (1927) *Animal Ecology*. University of Chicago Press, Chicago.
- 579 Emerson, B.C. & Gillespie, R.G. (2008) Phylogenetic analysis of community assembly and  
structure over space and time. *Trends in ecology & evolution*, 23, 619-630.
- Emmerson, M. & Yearsley, J.M. (2004) Weak interactions, omnivory and emergent food-web  
properties. *Proceedings of the Royal Society of London. Series B: Biological Sciences*,  
**271**, 397-405.
- 582 Etienne, R.S. & Haegeman, B. (2012) A conceptual and statistical framework for adaptive  
radiations with a key role for diversity dependence. *The American Naturalist*, **180**, E75-  
E89.
- 585 Foote, M. (1997) The evolution of morphological diversity. *Annual Review of Ecology and  
Systematics*, **28**, 129-152.
- 588 Ford, E. (1971) *Ecological genetics and evolution*. Springer.
- Fox, C.W., Roff, D.A. & Fairbairn, D.J. (2001) *Evolutionary ecology: concepts and case studies*.  
Oxford University Press.
- 591 Gillespie, R. (2004) Community assembly through adaptive radiation in Hawaiian spiders.  
*Science*, **303**, 356-359.
- 594 Goergen, E.M., Leger, E.A. & Espeland, E.K. (2011) Native perennial grasses show evolutionary  
response to *Bromus tectorum* (cheatgrass) invasion. *PLOS one*, **6**, e18145.
- Grant, B.R. & Grant, P.R. (1989) *Evolutionary dynamics of a natural population: the large  
cactus finch of the Galápagos*. University of Chicago Press.
- 597 Harmon, L.J. & Harrison, S. (2015) Species diversity is dynamic and unbounded at local and  
continental scales. *The American Naturalist*, 185, 584-593.
- 600 Harte, J., Rominger, A. & Zhang, W. (2015) Integrating macroecological metrics and community  
taxonomic structure. *Ecology letters*, **18**, 1068-1077.
- Helmus, M.R., Mahler, D.L. & Losos, J.B. (2014) Island biogeography of the Anthropocene.  
*Nature*, 513, 543.
- 603 Hendry, A.P. (2016) *Eco-evolutionary dynamics*. Princeton university press.

- 606 Herrera-Alsina, L., van Els, P. & Etienne, R.S. (2018) Detecting the dependence of  
diversification on multiple traits from phylogenetic trees and trait data. *Systematic  
biology*, **68**, 317-328.
- Hubbell, S.P. (2001) *A Unified Theory of Biodiversity and Biogeography*. Princeton University  
Press, Princeton.
- 609 Hubbell, S.P. (2013) Tropical rain forest conservation and the twin challenges of diversity and  
rarity. *Ecology and evolution*, **3**, 3263-3274.
- 612 Hughes, C. & Eastwood, R. (2006) Island radiation on a continental scale: exceptional rates of  
plant diversification after uplift of the Andes. *Proceedings of the National Academy of  
Sciences*, **103**, 10334-10339.
- 615 Hutchinson, G.E. (1965) *The ecological theater and the evolutionary play*. Yale University  
Press, New Haven.
- Huxley, J. (1942) *Evolution the modern synthesis*. George Allen and Unwin.
- 618 Jablonski, D. & Raup, D.M. (1995) Selectivity of end-Cretaceous marine bivalve extinctions.  
*Science*, **268**, 389-391.
- Jetz, W. & Fine, P.V.A. (2012) Global Gradients in Vertebrate Diversity Predicted by Historical  
Area-Productivity Dynamics and Contemporary Environment. *PLOS One*, **10**, e1001292.
- 621 Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis.  
*Trends in ecology & evolution*, **17**, 164-170.
- Kettlewell, H.B.D. (1955) Selection experiments on industrial melanism in the Lepidoptera.  
624 *Heredity*, **9**, 323.
- Krasnov, B.R., Mouillot, D., Shenbrot, G.I., Khokhlova, I.S., Vinarski, M.V., Korrallo-  
627 Vinarskaya, N.P. & Poulin, R. (2010) Similarity in ectoparasite faunas of Palaearctic  
rodents as a function of host phylogenetic, geographic or environmental distances: which  
matters the most? *International journal for parasitology*, **40**, 807-817.
- 630 Krasnov, B.R., Pilosof, S., Stanko, M., Morand, S., Korrallo-Vinarskaya, N.P., Vinarski, M.V. &  
Poulin, R. (2014) Co-occurrence and phylogenetic distance in communities of  
mammalian ectoparasites: limiting similarity versus environmental filtering. *Oikos*, **123**,  
63-70.
- 633 Krehenwinkel, H. & Tautz, D. (2013) Northern range expansion of European populations of the  
wasp spider *Argiope bruennichi* is associated with global warming–correlated genetic  
636 admixture and population-specific temperature adaptations. *Molecular ecology*, **22**, 2232-  
2248.
- Lande, R. (1979) Quantitative genetic analysis of multivariate evolution applied to brain-body  
size allometry. *Evolution*, **33**, 402-416.
- 639 Latham, R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests:  
energy-diversity theory does not account for variation in species richness. *Oikos*, 325-  
333.
- 642 Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943-1967.
- Levins, R. (1968) *Evolution in changing environments*. Princeton University Press, Princeton,  
NJ.
- 645 Losos, J. B. (2010). Adaptive radiation, ecological opportunity, and evolutionary determinism:  
American Society of Naturalists EO Wilson Award address. *The American Naturalist*  
648 **175**(6): 623-639.

- Losos, J.B. (2011) *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. Univ of California Press.
- 651 Lyons, S.K. (2003) A quantitative assessment of range shifts of Pleistocene mammals. *Journal of Mammalogy*, **84**, 385-402.
- 654 MacArthur, R. & Levins, R. (1964) Competition, habitat selection and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences*, **51**, 1207-1210.
- MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, **101**, 377-385.
- 657 MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, **100**, 603-609.
- 660 MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- MacArthur, R.H. (1961) Population effects of natural selection. *The American Naturalist*, **95**, 195-199.
- 663 MacArthur, R.H. (1962) Some generalized theorems of natural selection. *Proceedings of the National Academy of Sciences*, **48**, 1893-1897.
- MacArthur, R.H. (1969) Patterns of communities in the tropics. *Biological Journal of the Linnean Society*, **1**, 19-30.
- 666 Mahler, D.L., Revell, L.J., Glor, R.E. & Losos, J.B. (2010) Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution*, **64**, 2731-2745.
- 669 Makarieva, A.M. & Gorshkov, V.G. (2004) On the dependence of speciation rates on species abundance and characteristic population size. *Journal of biosciences*, **29**, 119-128.
- 672 May, R.M. (1974) *Stability and complexity in model ecosystems*, 2nd edn. Princeton University Press, Princeton.
- Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085-1093.
- 675 Mayr, E. & Provine, W.B. (1998) *The evolutionary synthesis: perspectives on the unification of biology*. Harvard University Press.
- 678 McCormack, J.E., Bowen, B.S. & Smith, T.B. (2008) Integrating paleoecology and genetics of bird populations in two sky island archipelagos. *BMC biology*, **6**, 28.
- McCormack, J.E., Huang, H., Knowles, L.L., Gillespie, R. & Clague, D. (2009) Sky islands. *Encyclopedia of islands*, **4**, 841-843.
- 681 McGill, B.J. & Brown, J.S. (2007) Evolutionary game theory and adaptive dynamics of continuous traits. *Annual Review of Ecology Evolution and Systematics*, **38**, 403-435.
- 684 McGill, B.J. (2019) The what, how and why of doing macroecology. *Global Ecology and Biogeography*, **28**, 6-17.
- McPeck, M.A. (2017) *Evolutionary community ecology*. Princeton University Press.
- 687 Metz, J.A.J., Geritz, S.A.H., Meszner, G., Jacobs, F.J.A. & van Heerwaarden, J. (1996) Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction. *Stochastic and spatial structures of dynamical systems* (ed. by S.J. Van Strien and S.M.V. Lunel), pp. 183-231. KNAW Verhandelingen, Amsterdam.
- 690 Millenium Ecosystem Assessment (2005) *Ecosystems and Human Well-being*. In. World Resources Insitute
- 693 Mittelbach, G.G. & Schemske, D.W. (2015) Ecological and evolutionary perspectives on community assembly. *Trends in ecology & evolution*, **30**, 241-247.

- 696 Moen, D. & Morlon, H. (2014) Why does diversification slow down? *Trends in Ecology & Evolution*, **29**, 190-197.
- Morgan, T.H. & Biologiste, Z. (1925) Evolution and genetics.
- 699 Moulton, M.P. & Pimm, S.L. (1983) The introduced Hawaiian avifauna: biogeographic evidence for competition. *American Naturalist*, **121**, 669-690.
- 702 Mutke, J., Sommer, J.H., Kreft, H., Kier, G. & Barthlott, W. (2011) Vascular plant diversity in a changing world: global centres and biome-specific patterns. *Biodiversity Hotspots*, pp. 83-96. Springer.
- Nosil, P. & Crespi, B.J. (2006) Experimental evidence that predation promotes divergence in adaptive radiation. *Proceedings of the National Academy of Sciences*, **103**, 9090-9095.
- 705 Nylin, S., Agosta, S., Bensch, S., Boeger, W.A., Braga, M.P., Brooks, D.R., . . . Nyman, T. (2018) Embracing colonizations: a new paradigm for species association dynamics. *Trends in ecology & evolution*, **33**, 4-14.
- 708 O'Neill, R.V. (1979) Transmutations across hierarchical levels. *Systems Analysis of Ecosystems* (G.S. Innis and R.V. O'Neill. (Eds.)), pp. 59-78.
- 711 Pantel, J.H., Bohan, D., Calcagno, V., David, P., Duyck, P.-F., Kamenova, S., . . . Thébault, E. (2017) 14 questions for invasion in ecological networks. *Advances in ecological research*, pp. 293-340. Elsevier.
- 714 Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, 111-117.
- Peterson, A. T., et al. (1999). Conservatism of ecological niches in evolutionary time. *Science* 285(20 August): 1265-1267.
- 717
- Pearse, I.S. & Altermatt, F. (2013) Predicting novel trophic interactions in a non-native world. *Ecology letters*, **16**, 1088-1094.
- 720 Phillimore, A.B. & Price, T.D. (2008) Density-dependent cladogenesis in birds. *PLoS biology*, **6**, e71.
- 723 Phillips, B.L., Brown, G.P., Webb, J.K. & Shine, R. (2006) Invasion and the evolution of speed in toads. *Nature*, **439**, 803.
- Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, **100**, 33-46.
- 726 Provine, W.B. (2001) The origins of theoretical population genetics: With a new afterword. University of Chicago Press.
- 729 Rabosky, D.L. & Lovette, I.J. (2008) Density-dependent diversification in North American wood warblers. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2363-2371.
- Rabosky, D.L. (2013) Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 481-502.
- 732 Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *PNAS*, **98**, 4534-4539.
- 735 Rangel, T.F., Edwards, N.R., Holden, P.B., Diniz-Filho, J.A.F., Gosling, W.D., Coelho, M.T.P., . . . Colwell, R.K. (2018) Modeling the ecology and evolution of biodiversity: biogeographical cradles, museums, and graves. *Science*, **361**, eaar5452.
- 738 Ricklefs, R. & Schluter, D. (1993a) Species diversity in ecological communities: historical and geographical perspectives. Chicago, University of Chicago, 414
- Ricklefs, R.E. & Cox, G.W. (1972) Taxon cycles in the West Indian avifauna. *The American Naturalist*, **106**, 195-219.



- 741 Ricklefs, R.E. & Schluter, D. (1993) Species diversity: regional and historical influences.  
Species diversity in ecological communities: historical and geographical perspectives (ed.  
by R.E. Ricklefs and D. Schluter). University of Chicago Press, Chicago.
- 744 Ricklefs, R.E. (1987) Community Diversity - Relative Roles of Local and Regional Processes.  
*Science*, **235**, 167-171.
- 747 Ricklefs, R.E. (2007) History and diversity: explorations at the intersection of ecology and  
evolution. *The American Naturalist*, **170**, S56-S70.
- 750 Ricklefs, R.E. (2010) Evolutionary diversification, coevolution between populations and their  
antagonists, and the filling of niche space. *Proceedings of the National Academy of  
Sciences*, **107**, 1265.
- 753 Ricklefs, R.E. (2011) Applying a regional community concept to forest birds of eastern North  
America. *Proceedings of the National Academy of Sciences*, **108**, 2300.
- 756 Roderick, G.K. & Navajas, M. (2003) Genes in new environments: genetics and evolution in  
biological control. *Nature Reviews Genetics*, **4**, 889.
- Roff, D. (2002) Life history evolution. Sinauer Associates, Sunderland, MA.
- 759 Rominger, A., Overcast, I., Krehenwinkel, H., Gillespie, R., Harte, J. & Hickerson, M. (2017)  
Linking evolutionary and ecological theory illuminates non-equilibrium biodiversity.  
*arXiv preprint arXiv:1705.04725*,
- 762 Rosenzweig, M.L. & McCord, R.D. (1991) Incumbent replacement: evidence for long-term  
evolutionary progress. *Paleobiology*, **17**, 202-213.
- Rosenzweig, M.L. (1978) Competitive speciation. *Biological Journal of the Linnaen Society*, **10**,  
275-289.
- 765 Rummel, J.D. & Roughgarden, J. (1983) Some differences between invasion-structured and  
coevolution-structured communities: a preliminary theoretical analysis. *Oikos*, **41**, 477-  
486.
- 768 Rummel, J.D. & Roughgarden, J. (1985) A theory of faunal buildup for communities. *Evolution*,  
**39**, 1009-1033.
- Schluter, D. (2000) *The ecology of adaptive radiation*. OUP Oxford.
- 771 Schoener, T.W. (2011) The newest synthesis: understanding the interplay of evolutionary and  
ecological dynamics. *science*, **331**, 426-429.
- 774 Sepkoski, J.J. (1978) A kinetic model of Phanerozoic taxonomic diversity I. Analysis of marine  
orders. *Paleobiology*, **4**, 223-251.
- 777 Shine, R., Brown, G.P. & Phillips, B.L. (2011) An evolutionary process that assembles  
phenotypes through space rather than through time. *Proceedings of the National Academy  
of Sciences*, **108**, 5708-5711.
- 780 Slik, J.F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L.F., Ashton, P., . . .  
Van Den Berg, E. (2015) An estimate of the number of tropical tree species. *Proceedings  
of the National Academy of Sciences*, **112**, 7472-7477.
- 783 Stanley, S.M. (1975) A theory of evolution above the species level. *Proceedings of the National  
Academy of Sciences*, **72**, 646-650.
- 786 Stearns, S.C. (1976) Life-history tactics: a review of the ideas. *The Quarterly review of biology*,  
**51**, 3-47.
- Stephens, D.W. & Krebs, J.R. (1986) *Foraging theory*. Princeton University Press, Princeton,  
NJ.

- Stommel, H. (1963) Varieties of oceanographic experience. *Science*, **139**, 572-576.
- 789 Stroud, J. T. and J. B. Losos (2016). Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* 47.
- 792 Ter Steege, H., Pitman, N.C., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., . . . Molino, J.-F. (2013) Hyperdominance in the Amazonian tree flora. *Science*, **342**, 1243092.
- 795 Turbelin, A.J., Malamud, B.D. & Francis, R.A. (2017) Mapping the global state of invasive alien species: patterns of invasion and policy responses. *Global Ecology and Biogeography*, **26**, 78-92.
- 798 Ulrich, W., Kusumoto, B., Shiono, T. & Kubota, Y. (2016) Climatic and geographic correlates of global forest tree species–abundance distributions and community evenness. *Journal of vegetation science*, **27**, 295-305.
- 801 Vermeij, G.J. (1996) An agenda for invasion biology. *Biological conservation*, **78**, 3-9.
- 804 von Humboldt, A. & Ross, T. (1852) Personal Narrative of Travels to the Equinoctial Regions of America, During the Years 1799-1804. HG Bohn.
- 807 Wagner, C.E., Harmon, L.J. & Seehausen, O. (2012) Ecological opportunity and sexual selection together predict adaptive radiation. *Nature*, 487, 366.
- 810 Wagner, C.E., Harmon, L.J. & Seehausen, O. (2014) Cichlid species-area relationships are shaped by adaptive radiations that scale with area. *Ecology Letters*, 17, 583-592.
- 813 Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385-397.
- 816 Wiens, J. J. and C. H. Graham (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* 36: 519-539.
- 819 Willis, A., Memmott, J. & Forrester, R. (2000) Is there evidence for the post-invasion evolution of increased size among invasive plant species? *Ecology Letters*, **3**, 275-283.
- 822 Wilson, E. & Bossert, W. (1971) A primer of population biology. *Sinauer Associates, Sunderland, MA*, **3**, 5.
- 822 Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist*, 95, 169-193.
- 822 Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston Jr, N.G. (2003) Rapid evolution drives ecological dynamics in a predator–prey system. *Nature*, **424**, 303.
- 822 Zillio, T., Banavar, J.R., Green, J.L., Harte, J. & Maritan, A. (2008) Incipient criticality in ecological communities. *Proceedings of the National Academy of Sciences*, **105**, 18714-18717.