Unifying macroecology and macroevolution to answer fundamental questions about biodiversity

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Unifying macroecology and macroevolution to answer fundamental questions about biodiversity

30th Anniversary of Macroecology contribution at *Global Ecology and Biogeography*

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Abstract

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 20th 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.

Historical Context

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 20th 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 20th 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).

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 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 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 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; McPeek, 2017; Schoener, 2011)(Metz *et al.*, 1996; McGill & Brown, 2007).

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 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 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.

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; 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. 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 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.

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).

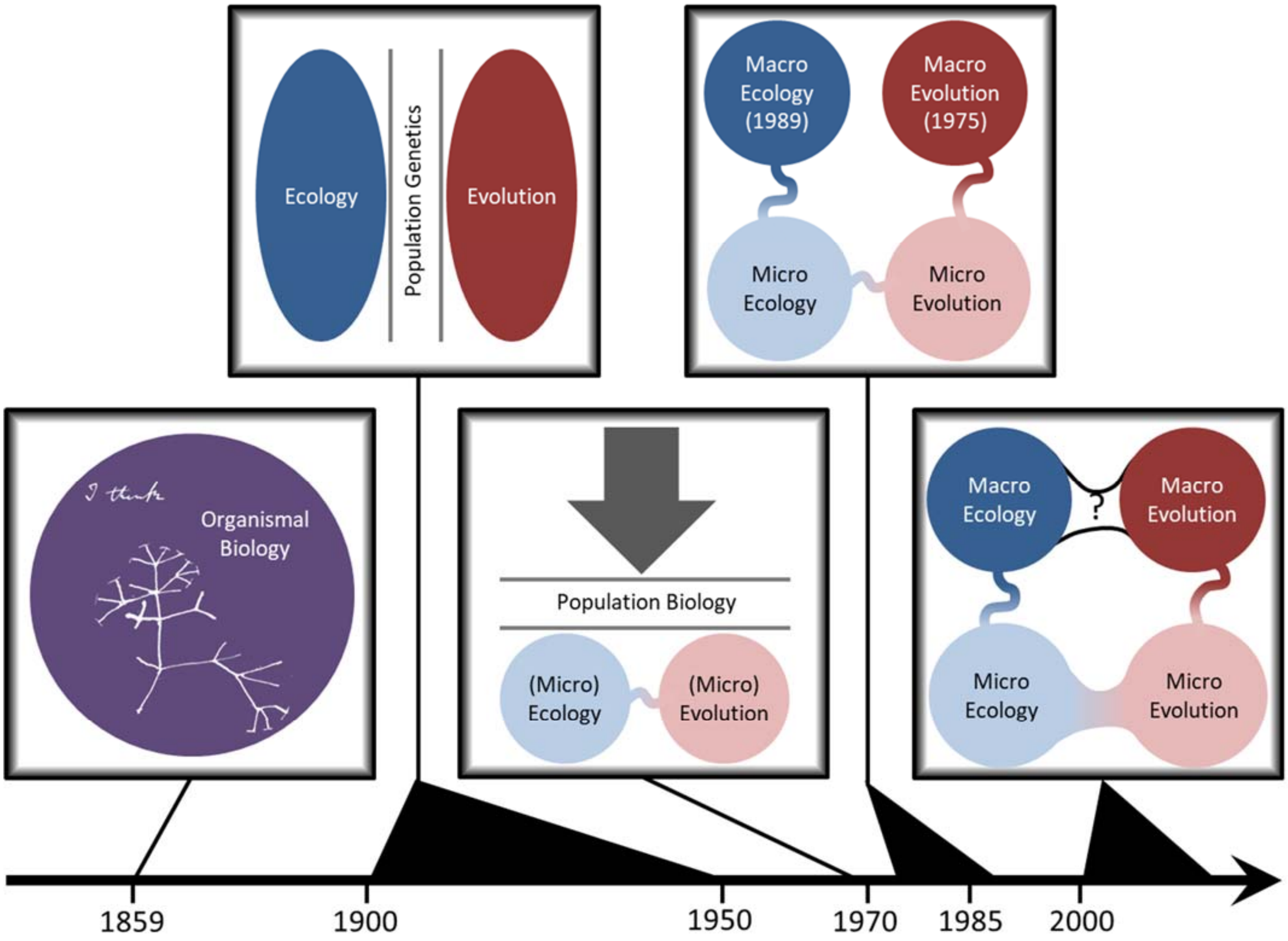


Figure 1 – A brief history of how Darwin's integrative vision of organismal biology became split into first two and then four separate fields: microevolution, macroevolution, micro-ecology (traditional population and community ecology), macroecology. In the bottom right panel, efforts to link microevolution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

Relationship of macroecology and macroevolution

Are we on our way to the seamless integration of ecology and evolution practiced by Darwin? We would suggest not yet in an important way. The missing linkage in the history as described above is a direct linkage between macroecology and macroevolution (question marks, Figure 1), despite seeming a natural link given their strong match in embracing large scales. Notably, the vertical linkages of the two macro-micro bridges have proven surprisingly resistant to advances (notwithstanding some successes (Avise, 2000), and we suggest they will ultimately prove to be harder barriers to cross than the ecology-evolution divide (hence the thicker line in Figure 1) for some specific mathematical reasons (O'Neill, 1979; McGill, 2019). Regardless of one's view on the feasibility of spanning the macro/micro divide, the indirect, 3-legged route of linking macroevolution to microevolution to microecology to macroecology is hopelessly unwieldy. **The main thesis of this paper is that organismal biology is missing - and badly needs - a re-unification directly between macroecology and macroevolution.**

A very simple examination of the limited interactions between macroecology and 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 Stanely'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

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.

- 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) .
- 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).
- 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)
- 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)
- Ricklef'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.

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 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 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.

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 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 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 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 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 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.

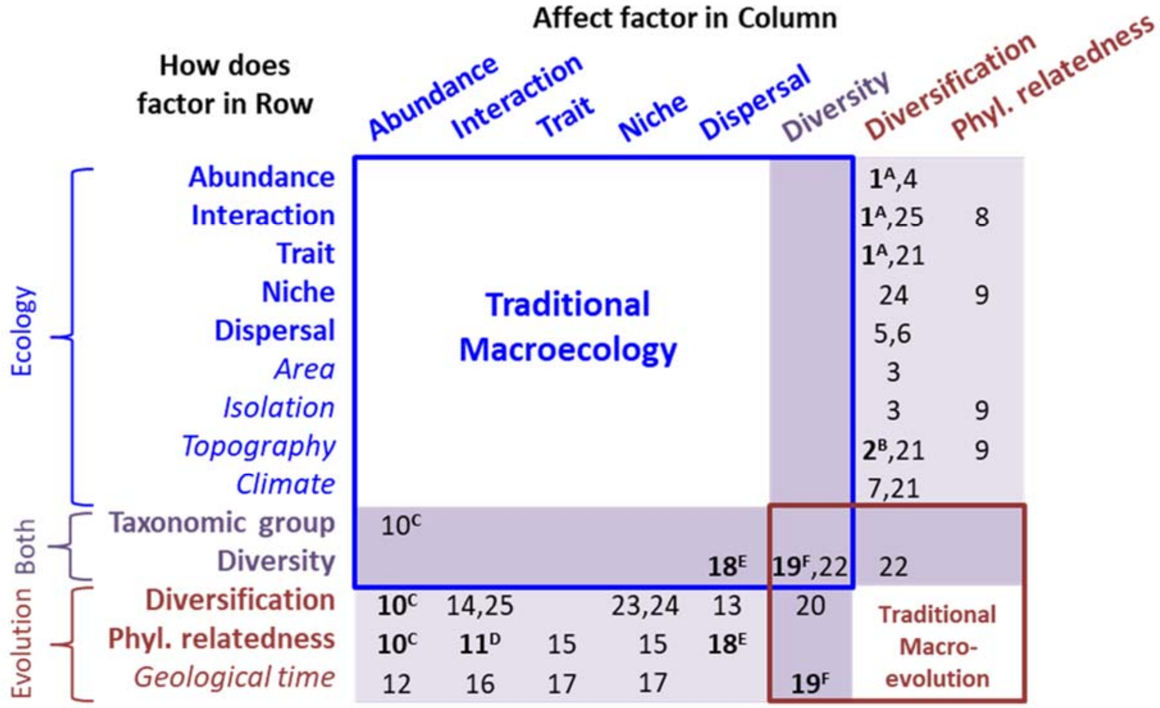
	Macroecology	**Macroevolution**
Diversity	Richness, evenness, abundance (often of polyphyletic groups)	Richness (typically within a monophyletic clade)
Traits	Morphospace, trait volumes and niches across an assemblage, functional diversity	Evolution of morphospace, trait volumes and niches across a phylogeny
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

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

As just shown, the overlap in concepts of interest to both macroecology and macroevolution hides deeper divides. Methodological challenges exist due to their disparate data 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

Scientific inquiry does not arbitrarily divide itself into spatial questions vs. temporal questions. Nor does scientific inquiry limit itself to a single source of data at a time. These are human created barriers. Although there may have been pragmatic reasons (including social and 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 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 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 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 the questions to provide more depth.



	How does factor in Row	Abundance	Interaction	Trait	Niche	Dispersal	Diversity	Diversification	Phyl. relatedness
Ecology	**Abundance**							**1**^{A},4	
	Interaction							**1**^{A},25	8
	Trait							**1**^{A},21	
	Niche							24	9
	Dispersal							5,6	
	Area							3	
	Isolation							3	9
	Topography							**2**^{B},21	9
	Climate							7,21	
Both	**Taxonomic group**	10^{C}							
	Diversity					**18**^{E}	**19**^{F},22	22	
Evolution	**Diversification**	**10**^{C}	14,25		23,24	13	20		
	Phyl. relatedness	**10**^{C}	**11**^{D}	15	15	**18**^{E}			
	Geological time	12	16	17	17		**19**^{F}		

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.

Ecological factors affecting evolution	
1	**What ecological conditions enable radiations? (case study A)**
2	**How do diversification rates scale with topography? (case study 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?
Evolutionary factors affecting ecology	
10	**How do relative abundance patterns respond to macroevolution? (case study C)**
11	**Are ecological interactions determined by shared evolutionary history? (case study D)**
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?
Cross cutting questions	
18	**What is the role of evolution in invasion? (case study E)**
19	**Does diversity saturate in space and/or time? (case study F)**
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?

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.

Case Studies

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.

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

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 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 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 & 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 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 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.*, 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 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.

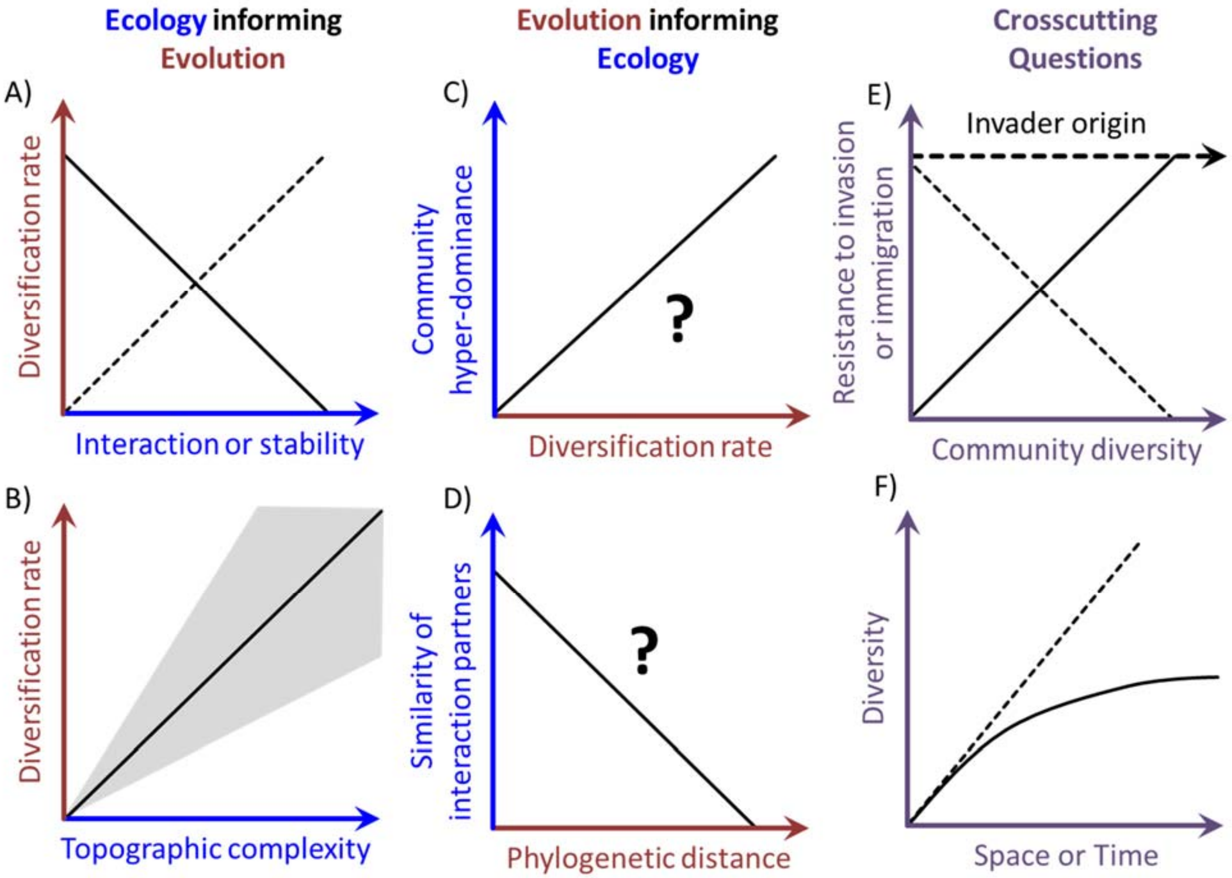


Figure 3. Hypothetical relationships between driver and response variables for six case studies taken from Table 2. The first column represents case studies A and B where ecological factors primarily influence evolutionary patterns and processes. The second column represents case studies C and D where 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.

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

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 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 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 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 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.*, 2008).

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 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 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 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 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 of these ecological factors cause, or are caused by, the evolutionary processes leading to high diversity remains an open question.

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 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 host parasite interactions in particular, on the one hand, there is evidence that differences in 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 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 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 Question 8 is qualitatively the same question with ecology driving evolution.

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

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 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 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 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 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 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 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 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 invasion may be spatially structured (e.g. different at the invasion front) (Shine *et al.*, 2011) or admixtures (geographic hybrids)(Krehenwinkel & Tautz, 2013). The species in the invaded community may also show an evolutionary response to the invader (Goergen *et al.*, 2011) or 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.

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.

Conclusions

The modern push to reconnect ecology to evolution (Hendry, 2016; McPeek, 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.

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