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perspective

Differences between regional and biogeographic species pools highlight the need for multi-scale theories in macroecology

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Abstract. Ecologists are intrigued by the manner in which colonists from a regional pool of species establish and structure local ecological communities. This has initiated several approaches to identifying the relative roles of regional and local processes. Recently, large-scale data sets and novel statistical tools have sparked renewed interest in objectively defined homogeneous species pools. At continental and global scales, these homogenous units are known as biogeographic species pools. Here we argue that the biogeographic species pool is not just a scaled-up version of the regional species pool featured in many foundational ecological theories. Instead, the processes linking local communities and regional species pools differ from those in the biogeographic species pool. To illustrate this, we distinguish between regional and biogeographic species pools by overlaying species distribution data and differentiating between the intersection and union of these distributions. Although patterns in the regional and biogeographic species pools may appear self-similar across scales, the underlying mechanisms differ from those between local communities and the regional species pool. As a consequence, conventional approaches of quantifying the relative role of local and regional process are inappropriate for studying the biogeographic species pool, thus highlighting the need for new multi-scale theories in macroecology.

Keywords. Anura, emergent properties, extent of occurrence, hierarchical spatial scales

Introduction

The regional species pool is the set of species that can potentially colonize and establish within a local community (Lessard et al. 2012a). Ecologists use information from the regional species pool to quantify the role of evolutionary history in shaping contemporary patterns of local species assemblages. Several foundational theories in community ecology assume that local patterns are contingent on the colonization dynamics from a regional source of migrants (MacArthur and Wilson 1967, Hubbell 2001). These theories assume that speciation and historical dispersal add species to the regional species pool, which are then passed through a series of ecological 'filters' to form local assemblages (Guisan and Rahbek 2011). These filters include the dispersal ability of a species, which determines whether individuals can reach the local assemblage; local abiotic conditions that, along with the individual's physiological constraints, permit the establishment, survivorship and reproduction of populations; and species interactions, which modulate resource availability, competition, predation and pathogens (Soberón 2007, Soberón and Nakamura 2009). The relative importance of these three classes of filters probably depends on the spatial scale (interpreted as the grain size of the relevant diversity pattern: Whittaker et al. 2001, Scheiner 2011) at which the local assemblage is studied (Lawton 1999, Schneider 2001, Hortal et al. 2010, McGill 2010).

Ecologists scrutinise the relationship between local and regional diversity patterns to identify the roles of historical evolutionary processes and contemporary ecological filters in structuring communities (Ricklefs 1987, Harrison and Cornell 2008, Belmaker and Jetz 2012). They do so either by plotting and analysing the relationship between regional and local diversity patterns on separate axes (Ricklefs 1987) or by using reshuffling algorithms to identify patterns in the local community expected from random chance for any given regional species pool (Connor and Simberloff 1979). The former approach assumes that local community processes—i.e., species sorting and species interactions—are less important than regional processes—i.e., speciation and historical dispersal—in shaping local communities when local and regional diversity patterns are linearly related (Ricklefs 1987, Lawton 1999). In contrast, local processes supposedly outweigh regional processes when local diversity is asymptotically related to regional diversity (Ricklefs 1987, Lawton 1999). In the latter approach, observed patterns in local communities are contrasted to those simulated by null models to disentangle deterministic patterns of community assembly from random expectations (Chase and Myers 2011, Myers et al. 2013). Both approaches depend on how the regional species pool is defined geographically. This ultimately determines the relationship between local and regional diversity and can potentially change how results are interpreted (Graves and Gotelli 1983, Lessard et al. 2012b).

Carstensen et al. (2013) realised that the geographical delineation of the regional source pool is the crucial first step to studying the interplay between local and regional diversity patterns. They advocated a regional source pool delineated in a standardised way and reviewed three potential approaches to doing so: the assemblage dispersion field (Graves and Rahbek 2005) and homogeneous biogeographical regions identified using either distance-based clustering (Smith 1983, Kreft and Jetz 2010) or network modularity analysis (Carstensen and Olesen 2009). However,

Box 1. Glossary

Area of occupancy (AOO): The geographical area within the extent of occurrence where a species actually occurs (Fig. 2c). The AOO is, therefore, smaller than the extent of occurrence and signifies the realised geographical distribution.

Assemblage dispersion field: A graphic depiction of the range-wide geographical distribution of all species that co-occur in a given assemblage. It is one representation of the biogeographic species pool (Fig. 3).

Biogeographical scale: A collective term for spatial scales greater than the geographic area of the discrete regional species pool. These scales, therefore, incorporate multiple regional species pools.

Biogeographic species pool: A conceptual representation of the geographical area in which the composition of aggregated assemblages are more similar (homogenous) than assemblages from outside the geographical area.

Discrete regional species pool: The geographical area within which any two (or more) randomly selected points will have the same regional species pool (Fig. 3).

Ecological filter: An ecological process that constrains the local establishment of species from a regional species pool.

Extent of occurrence (EOO): A geographical representation of the outer limits of species occurrence, which signifies the potential range of a species (Fig. 2b).

Local scale: A generic term for the spatial scale at which individuals of a species interact with one another and with their biotic and abiotic surroundings. It is, therefore, a fluid concept that varies depending on the species.

Point scale: The spatial scale at which individual organisms respond to immediate stimuli while primarily being constrained by processes at the local scale.

Regional scale: The collective term for spatial scales smaller than the area of the discrete regional species pool, but larger than the local scale, where all communities are subsets of the same list of potential colonists (i.e., the same regional species pool)

Regional species pool: A set (list) of species that can potentially colonize and establish within a community.

Scale: In the context of this study, scale refers to the grain (also called focus) of the biological pattern. In cases where data are aggregated over multiple sampling units, scale refers to the aggregated property, not the dimensions of the sampling unit. Although scale is a continuous concept, this study distinguishes between biogeographical, regional, local and point scales.

these aggregated assemblages are regularly based on large geographic regions, so Carstensen et al. (2013) coined a new term for these units: biogeographic species pools (Box 1).

Biodiversity is nested hierarchically across spatial scales (Noss 1990), so it is easy to envisage a hierarchy where local communities are nested within regional species pools, which are nested within the biogeographic species pool. At first glance, these spatial scales appear self-similar: regional-scale patterns seem to be associated with biogeographical-scale patterns in much the same way local-scale patterns are associated with regional-scale patterns. However, we believe that this convenient arrangement of ecological units across spatial scales is a red-herring. While it is reasonable to assume that local community patterns are the result of ecological filters imposed on a regional pool of potential colonists, the same cannot be said for the biogeographic species pools. It is unlikely that there is a global or continental pool of species from which communities draw migrants (Ricklefs and Renner 2012), so the causal link from the biogeographical region to the regional species pool (or finer spatial scales) through a series of ecological filters seems misconstrued. As a consequence, we should avoid applying conventional analytical tools (e.g., regional-local regression and random reshuffling) to the biogeographic species pool.

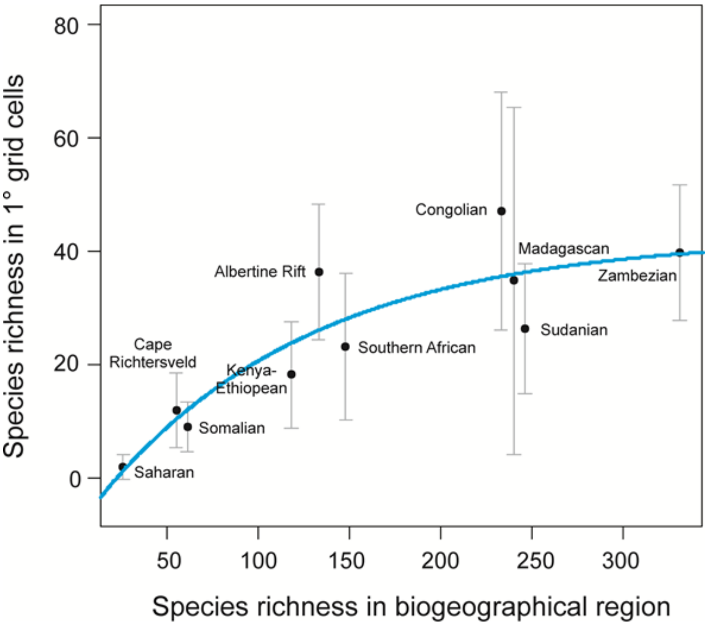

Figure 1. The asymptotic relationship between the total Amphibian species richness of biogeographical regions in Africa and the average species richness of 1° grid cells within those regions (error bars show the standard deviation). Unlike the relationship between local community diversity and diversity in the regional species pool, this asymptotic relationship cannot not be interpreted as evidence of deterministic ecological filters because it has already been demonstrated how historical speciation processes underlie richness in 1° grid cells (e.g., Buckley and Jetz 2007, Pyron and Wiens 2013). The biogeographical regions were delineated by Linder et al. (2012).

For example, correlations between regional-scale patterns, such as species richness in 1° grids cells, and biogeographical-scale patterns, such as the richness in a homogeneous biogeographical region (Linder et al. 2012), should not be interpreted in the conventional sense. For instance, amphibian richness in 1° grid cells (approximately 10 000 km^2) across Africa have an asymptotic relationship with the total richness of the biogeographical region within which they are nested (Fig. 1). However, to attribute this relationship to deterministic ecological filters would be short-sighted because we already know that patterns of amphibian diversity in 1° cells are due to geographical variation in historical rates of diversification, extinction and dispersal (Buckley and Jetz 2007, Pyron and Wiens 2013). Furthermore, to attribute this asymptotic relationship to a uniform set of ecological filters is an oversimplification because the relative importance of environmental and spatial processes varies between biogeographical regions in Africa (Buschke et al. 2014). Similarly, reshuffling species occurrence patterns within the whole Afrotropical realm will overestimate the importance of ecological filters unless it explicitly considers the effect of the historical processes responsible for patterns of biogeographical provincialism (e.g., Linder et al 2012).

In their presentation of the biogeographic species pool, Carstensen et al. (2013) cautioned against using the biogeographic species pool to study community structure using conventional approaches because these might overestimate the ability of species to colonize any point within the pool. We agree with this sentiment wholeheartedly and believe that this caveat needs to be considered more explicitly. In the following, we explain why the biogeographic species pool is not just a scaled-up version of the regional species pool by describing a simple example at the population level. This raises the question of distinguishing between regional and biogeographic species pools and, more importantly, identifying the scale at which it is no longer appropriate to use conventional analytical tools to assess the importance of ecological filters. To this end, we propose a new way of distinguishing between regional and biogeographic species pools by overlaying species distribution maps and identifying the geographical extent of the regional species pool. We end by briefly discussing the various factors determining the geographical extent of the regional species pool and suggesting ways in which these factors can be related back to the biogeographic species pool.

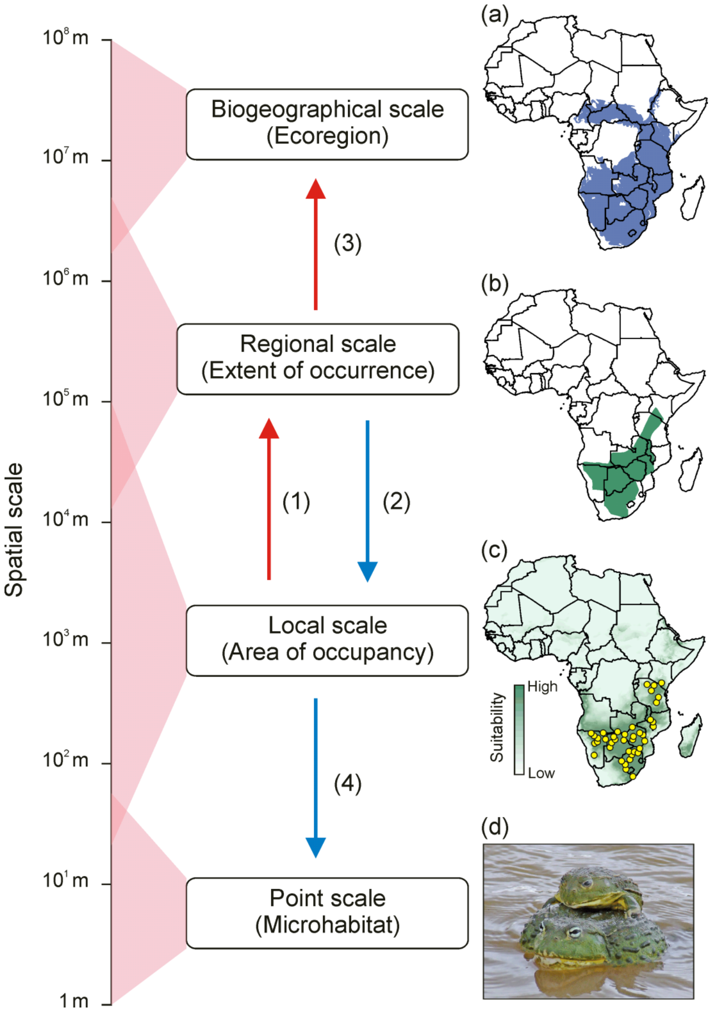

Figure 2. The hierarchical distribution of the African bullfrog, *Pyxicephalus adspersus*, **(a)** from the biogeographical scale, determined as the ecoregions in which the species occurs; **(b)** regional scale, represented as the extent of occurrence; **(c)** local scale, denoted by point localities of occurrences and estimated habitat suitability; **(d)** and the point scale, which incorporates the short-term movements of individuals between microhabitats. Numbered arrows suggest ways in which patterns may interact at different scales.

Linking patterns across scales: population level

If the regional species pool is the collection of species that can potentially colonize and establish within a local community, then there should also be an analogous unit at the population level. We believe that the species distribution range expressed as the extent of occurrence (EOO) is the population analogue of the regional species pool. EOO data are usually compiled by experts who create range maps from decades of inventories across numerous localities (Whittaker et al. 2001) and thus exaggerate the distribution because it implies that the species has the potential to occupy a region, not that it actually occurs there (Hortal 2008). The EOO signifies the outermost geographic limits of species occurrence and should be distinguished from the area of occupancy (AOO), which represents the area in which a species actually occurs (Gaston 2003, Gaston and Fuller 2009). As a consequence, a species' AOO is usually considerably smaller (40-65%) than its EOO (Hurlbert and Jetz 2007). Moreover, the EOO does not necessarily signify the outer limits of a single metapopulation, so populations at opposite edges of the EOO are not always linked by dispersal .

To illustrate the concept of a population equivalent of the regional species pool, we use the African bullfrog, *Pyxicephalus adspersus*, as a case example. These frogs are endemic to the arid and subtropical grasslands and savannas of southern Africa and spend the majority of the year underground in a state of torpor, emerging only for a brief window after exceptional summer rains to spawn in ephemeral wetlands (Cook et al. 2001). The distribution range for this species is structured hierarchically (Fig. 2: see supplementary appendix for details of the data used to describe these distributions). It must be emphasized, however, that this specific hierarchical structure is intended to be illustrative, which means that the precise scaling and data sources are open for interpretation.

We define the local scale as the scale at which individuals of a species interact with each other and with their biotic and abiotic surroundings. At local scales, point localities represent areas where individual frogs occur (Fig. 2c). Processes occurring at the local scale (e.g., births, deaths, and migration between breeding and overwintering sites) determine the AOO of these frogs. The aggregated effects of reproduction, range expansion and local extinction over several generations combine to determine the bullfrogs' EOO (Gaston 1998, 2003, Holt and Keitt 2000). In this sense, processes at the local scale influence patterns at the regional scale (upward arrow 1 in Fig. 2). However, processes at the regional scale may also affect patterns at the local scale in instances where large-scale, historical processes influence local occurrence patterns (downward arrow 2 in Fig. 2). For instance, an unoccupied and suitable habitat within the EOO can be colonized by the African bullfrog, but the same cannot be said for a favourable wetland way beyond the outer limits of the EOO. Of course, the EOO is a dynamic entity that can expand and contract. However, since it represents aggregated patterns over several generations, its boundaries will remain relatively stable at time-intervals relevant to individual organisms due to regression toward the mean over extended time periods. We believe that the interdependence between local occurrences and the outer boundaries of distribution ranges (*sensu* Ficetola et al. 2014) is the population analogue of the interplay between local communities and the regional species pool.

For the purposes of this illustrative example, we chose to define the biogeographical distribution of the African bullfrog (Fig. 2a) as the spatial extent of the ecoregions in which this species occurs (Olson et al. 2001). This choice is not definitive and it would be equally appropriate to define this range as the biogeographical realm (Procheş and Ramdhani 2012, Holt et al. 2013) or region (Linder et al. 2012) in which the species occurs. Regardless of how the biogeographical range is defined, it should be viewed as an emergent property of patterns and processes at smaller spatial scales (upwards arrow 3 in Fig. 2). Salt (1979) defined an emergent property of a complex ecological system as the property which is wholly unpredictable from observation of the components of that unit. In complex systems, emergence implies upward causation because self-organised patterns 'emerge' from the swarm of interactions between constituent parts at smaller scales (Levin 2005).

Contrastingly, patterns at the point scale (Hortal et al. 2010) are primarily affected by patterns and processes at larger spatial scales (downward arrow 4 in Fig. 2). Patterns at the point scale represent the actual positioning of individual organisms in response to immediate stimuli. For example, the positioning of wood-decaying fungi on a decaying log may be influenced by biotic interactions and the abiotic attributes of the log (Ovaskainen et al. 2010). However, these processes play a secondary role in the distribution of fungi, which is ultimately constrained by the species identity of the host tree regardless of the suitability at the point scale (Ovaskainen et al. 2010). In the case of the African bullfrog, the tendency of tadpoles to aggregate in shallower waters where temperature and oxygen concentrations are more suitable for rapid development. The choice of microhabitat (point scale) is constrained by the choice of wetland (local scale), not the other way around. In fact, adult frogs must resort to modifying the microhabitat at the point scale by digging canals between isolated puddles to ensure inflow of colder, oxygen rich water from the larger pool (Kok et al. 1989, Cook et al. 2001).

To summarise, we suggest that local processes (e.g., births, deaths and migration) may influence regional distribution patterns (EOO) while regional processes (speciation and historical range expansion) simultaneously affect local ecological patterns (by geographically constraining the colonization and establishment of local populations). This creates a feedback loop between local and regional processes and, as a consequence, both statistical and conceptual associations between population patterns at local and regional scales. Contrastingly, patterns at the scale of biogeographical regions are the aggregated effect of processes occurring at smaller scales, not the other way around. Any associations, therefore, reflect the consequences of bottom-up causal processes. Similarly, the short-term movements of individuals within local scales are primarily constrained by processes occurring at larger spatial scales and, therefore, reflect top-down causality.

Linking patterns across scales: community level

Defining the regional species pool

The hierarchical structuring of populations (Fig. 2) seems intuitive, but as is so often the case in ecology, it is complicated by the inclusion of additional species. If the EOO is the population analogue of the regional species pool, then the regional species pool for multiple species should also incorporate the EOOs for each of the constituent species. We propose that the 'intersection' and 'union' of EOOs demonstrate the differences between the regional and biogeographic species pools (Fig. 3). In the simplest case of two species, much like a Venn diagram, the outcome of two intersecting ranges is three separate species pools: a portion where only the first species occurs, a portion where only the second species occurs and the intersection where both species co-occur. The union of EOOs, on the other hand, represents the outer limits of the assemblage dispersion field (Graves and Rahbek 2005), which is one way of delineating the biogeographic species pool (Carstensen et al. 2013).

Although we argue that the intersection of EOOs is a geographically discrete way of defining the regional species pool, we should perhaps elaborate further on the exact meaning of this statement. The regional species pool is a set of species that can potentially colonize and establish locally and should thus be seen as a list of species (Figure 3). The intersection of EOOs is the geographical space within which any randomly se-

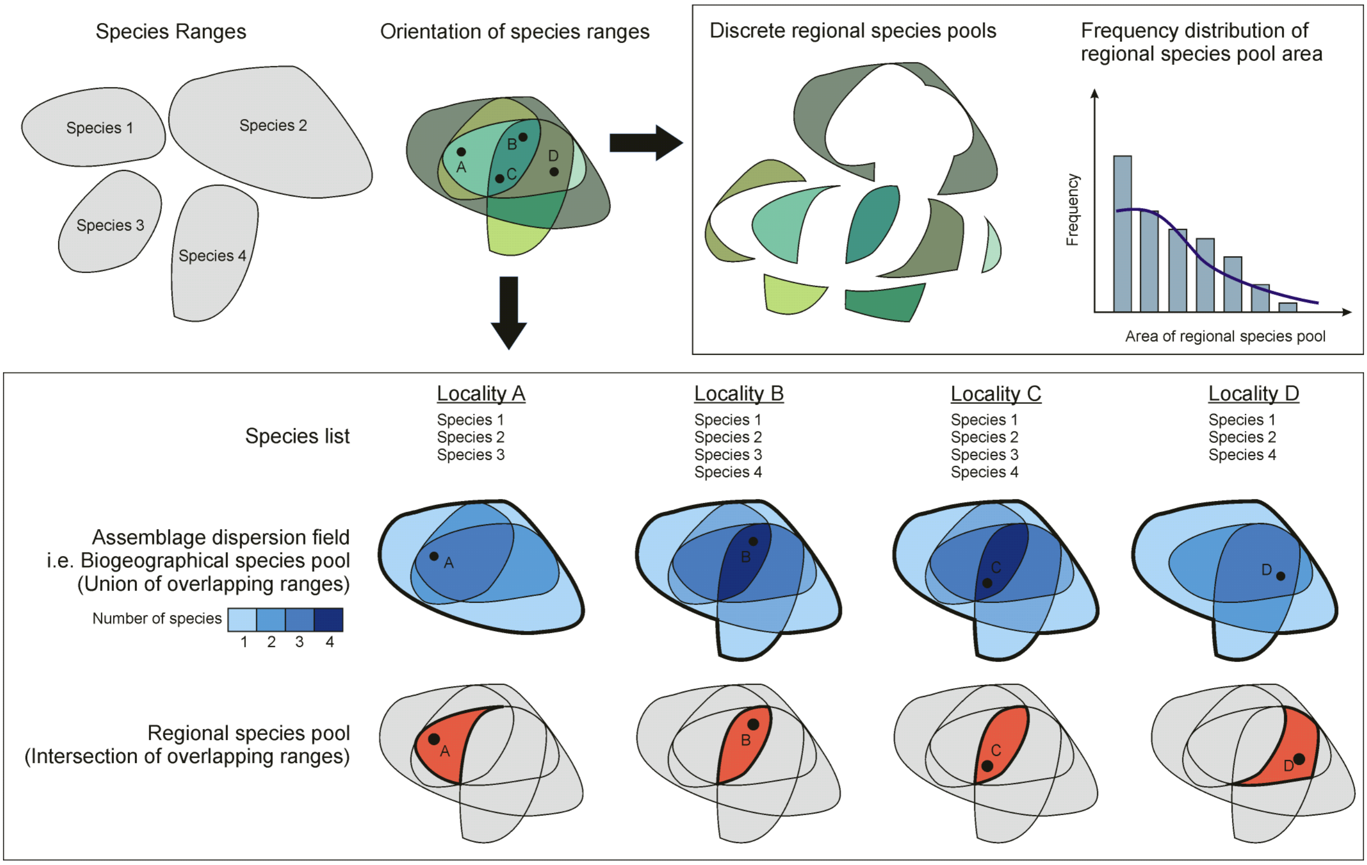

Figure 3. Conceptual view of the intersection of four species ranges (species 1–4) and how this influences the list of potential colonists, the biogeographic species pool (defined as the assemblage dispersion field) and the discrete regional species pool at four localities (localities A–D). In addition, the frequency distribution can be calculated for the discrete regional species pools caused by the intersection of four species ranges.

lected point localities will have the same set of potential colonists (i.e., the same regional species pool). This discrete regional species pool does not represent the outer geographical limits from which potential migrants will be drawn. Local assemblages are open to colonization by independent populations of species (Leibold et al. 2004, Ricklefs 2008), so the outer boundary for potential colonists will be determined by the distribution and dispersal ability of individual species. In this regard, the assemblage dispersion field is perhaps a better representation of the outer limits of potential colonists, but even this is not necessarily true when the EOO contains multiple independent metapopulations.

Defining the regional species pool as intersecting EOOs has several immediate consequences. The first is that the scale of a regional species pool can be viewed as a discrete entity with clearly defined boundaries determined by the range edges of the constituent species. It therefore makes sense to attribute differences in diversity patterns within this discrete pool to ecological filters because all localities share a common regional species pool. Contrastingly, when comparing patterns across two or more discrete pools, the effects of ecological filters can potentially be mistaken for those caused by the historical factors which shape the regional species pool.

A second consequence of defining discrete species pools by intersecting EOOs is that the surface area of the pool will generally decrease as more species are added and that the maximum size of the species pool is constrained by the range size of the most narrowly distributed species in the pool. A simple way to illustrate this is to calculate the probability of any combination of species co-occurring by multiplying the area of their ranges proportional to the study domain (Mokany and Paini 2011). For instance, the random expectation of two species co-occurring when each covers half the study domain is 0.5 x 0.5 = 0.25 and the expected area of sympatry is the area of the domain multiplied by 0.25. Similarly, adding a third species, which also covers half the study domain, would decrease the random expectation of three species in sympatry to 0.125 (0.5 x 0.5 x 0.5).

The final implication of the discrete regional species pool is that adjacent pools will generally only differ in composition by a single species although, in reality, the edges of many species' ranges may coincide at natural boundaries, such as rivers, mountains or habitat ecotones. As such, a shortcoming of delineating the discrete regional species pool by intersecting EOO, is that ecologists must use their own discretion when deciding whether the boundaries between two regional species pools are biologically meaningful or simply an artefact of misaligned EOO data. The similarity between adjacent discrete regional species pools demonstrates that they are not integral circumscribed ecological entities in the Clementsian sense (Clements 1936), but rather homogeneous units from which point estimates of overlapping species ranges can only be drawn (the local community according to Ricklefs 2004, 2008). Even though compositional differences between adjacent pools are small, they are not trivial. For instance, two local communities within adjacent regional species pools could have identical species composition, but they would differ in terms of dark diversity: the number of potential colonists from the regional community that are absent from a local community (Pärtel et al. 2011).

The ecological significance of the biogeographic species pool

At the population level we proposed that patterns at the biogeographical scale are emergent properties of patterns and processes occurring at smaller spatial scales. By extension, the multiple-species biogeographic pool should also be viewed as an emergent property of local and regional scale community patterns and processes. This certainly does not suggest that assemblage patterns at the biogeographical scale are uninformative. On the contrary, maps illustrating clearly defined biogeographical regions have captured the imagination of biogeographers since the earliest efforts of Wallace (1876) and have undoubtedly contributed to our understanding of biodiversity (e.g., Kreft and Jetz 2010, Linder et al. 2012, Procheş and Ramdhani 2012, Holt et al. 2013). Nevertheless, we should not mistake the biogeographic species pool for a scaled-up version of the regional species pool. More importantly, we should avoid applying ecological theory based on the colonization dynamics within regional species pools to biogeographic species pools.

Ecological and evolutionary processes underlying the regional species pool

The processes determining the degree to which species ranges overlap in each unique assemblage can be categorised based on the three major determinants of species ranges at the population level: speciation, range expansion and extinction (Gaston 1998, 2003). Evidently, the ranges of species originating from the same geographic locality are more likely to overlap because regions with high speciation rates tend to also have high species richness (Pyron and Wiens 2013). Speciation history, therefore, directly determines *which* species may exist in sympatry (i.e., which species occur in the regional species pool), but its influence on the *degree* of sympatry is less certain (i.e., the geographical area of the discrete regional species pool). Instead, the degree to which species ranges overlap is primarily determined by range expansion and subsequently on whether species are able to persist in its new habitat. This is determined by environmental conditions and biotic interactions. Environmental gradients not only influence the boundaries of individual species' ranges (Merriam 1894, Pigot et al. 2010), they also seem to affect the number of species that can co-occur (Hawkins et al. 2003, Field et al. 2009). The effect of biotic interactions on the regional species pool is less clear, especially at global and continental scales where studies of species interactions are very difficult to carry out (Wiens 2011). However, there is compelling new evidence that species interactions—most probably competitive interactions—can shape macro-scale species co-occurrence patterns (Gotelli et al. 2010, Pigot and Tobias 2013).

Speciation, dispersal, environmental constraints and species interactions all contribute to the degree of overlap for a set of species ranges and their relative importance may be dependent on scale (Hortal et al. 2010, McGill 2010, Guisan and Rahbek 2011). There is, however, probably much overlap and interaction

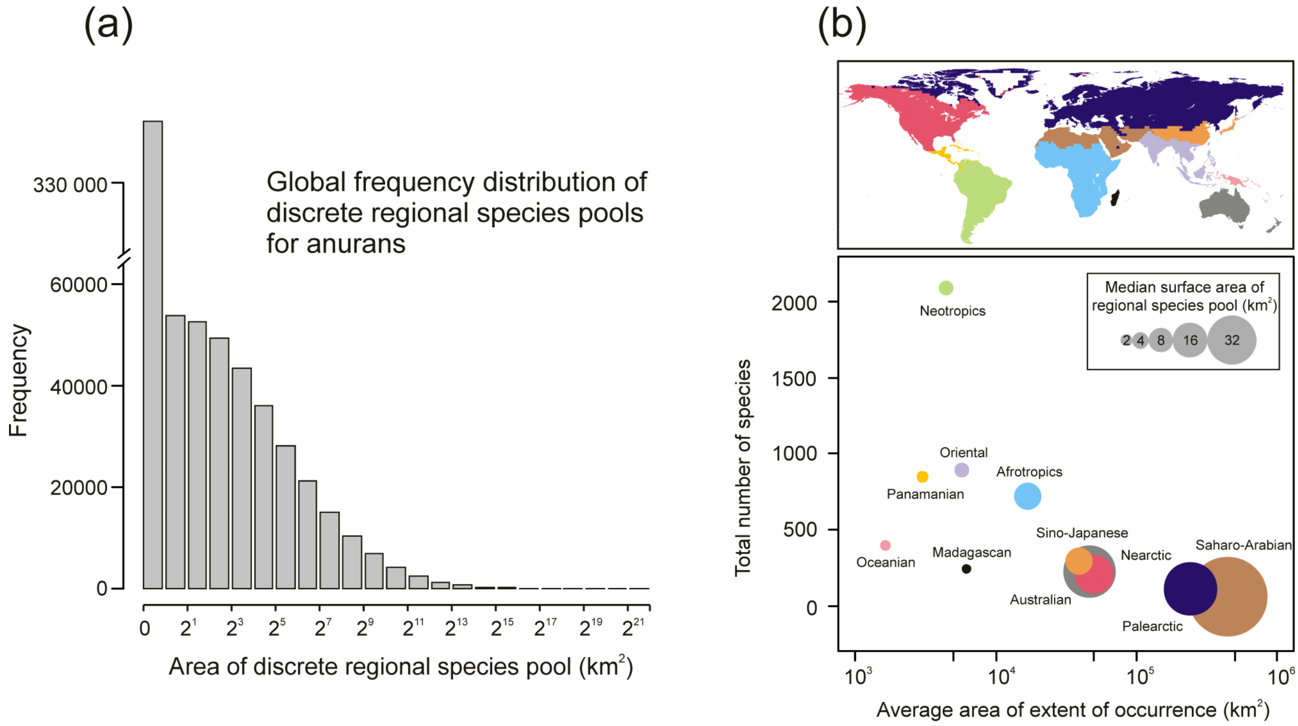

Figure 4. (a) The area frequency distribution for discrete regional species pools for 5459 Anuran species globally. **(b)** The relationship between the total number of species, the average surface area of their extents of occurrence (measured on a logarithmic scale) and the median surface area of the regional species pool (coloured circles) for Anuran species in biogeographical realms.

Box 2. Comparative studies of regional species pools

We compared the geographical extent of discrete regional species pools between biogeographical realms by overlaying the distribution ranges—expressed as the EOO—for 5459 anuran species at the global scale. Data were from the Global Amphibian Assessment by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species version 2009.1 (IUCN 2009). Overall, the area frequency distribution of discrete regional species pools was unimodal, strongly right-skewed and dominated by small surface areas (Fig. 4a). More than half the discrete regional species pools (341955 of 667256 discrete units) were smaller than 1 km^2, but we should not read too much into these precise values which may be errors caused by small inaccuracies in the spatial boundaries of EOO ranges. These errors occur when range limits do not coincide perfectly in instances where multiple species reach their natural range limits at clearly defined boundaries (such as rivers or habitat interfaces). To overcome the effects of these errors, we excluded the smallest frequency class (discrete species pools smaller than 1 km^2) in subsequent descriptive analyses.

We used a recent delineation of biogeographical units (Holt et al. 2013) to compare discrete regional species pools among realms. The median surface area of discrete regional species pools within each realm was contrasted with the number of species within that realm as well as the average EOO of those species measured on a logarithmic scale (Fig. 4b). Even from such a conceptually simple analysis, it is immediately apparent that the surface area of the regional species pool is larger when there are only few wide-ranging species. In parts of the Sahara Desert, for example, the ranges of only a handful of species, each with widespread distributions (the Sahara Frog, *Pelophylax saharicus*, the Sub-desert Toad, *Amietophrynus xeros*, and the Common Sand Frog, *Tomopterna cryptotis*), co-occurred in a regional species pool that covered an area of approximately 770500 km^2.

However, it is also evident that the median surface area of the regional species pool is not a simple function of species richness and range size. For example, the Neotropics, Oriental and Madagascar realms have similarly sized regional species pools (9.18 km^2, 9.09 km^2 and 4.1 km^2, respectively), comparable average range size (4400 km^2, 5683 km^2 and 6213 km^2, respectively), but widely different total species richness (2094, 890 and 240 species, respectively). This is suggestive of possible differences between the biogeographical processes within mainland continents, archipelagos and single landmass islands. As a counter example, the Sino-Japanese, Nearctic and Australian realms have differently sized regional species pools (29.61 km^2, 58.63 km^2 and 102 km^2, respectively), despite having similar numbers of anuran species (296, 201 and 223 species, respectively) with comparable average range sizes (39190 km^2, 50904 km^2 and 45964 km^2, respectively). These findings suggest that it may be possible to pin down the mechanisms underlying the extent of the regional species pool if we can identify how speciation, which determines the number of species in a realm, and colonization and extinction dynamics, which contribute to determining range sizes, vary among biogeographical realms.

across these scales because processes are likely also mutually dependent. For instance, dispersal limitation attributed to the Rift Valley has been offered as an explanation for diversification of African clawed frogs, *Xenopus*, in the Ethiopian highlands (Evans et al. 2011). Similarly, Salisbury et al. (2012) demonstrated that high rates of specialisation in tropical birds, presumably to reduce competition, limits dispersal across reproductive barriers and increases allopatric diversification rates. Moreover, these processes seem to be modulated by climatic variability, which has been proposed as the driving factor behind the trade-off between dispersal ability and ecological specialisation (Jocque et al. 2010). As a consequence, there are innumerable ways in which speciation, dispersal, environmental constraints and species interactions can combine to shape the regional species pool. Facing similar complexity, Vellend (2010) proposed the existence of a 'black box' in community ecology containing all the unidentifiable ways in which patterns and process can be linked. He further speculated this box contains no generalities, but rather conclusions that are fundamentally system-specific. If Vellend's (2010) arguments also apply to the regional species pool, then a comparative study of specific cases would perhaps be more fruitful than one grounded in general theory (Box 2).

Conclusion

Patterns in the biogeographic species pool may resemble scaled-up versions of the regional species pool, but this should not be mistaken for evidence of similar underlying processes. As a consequence, the well-studied tools for quantifying the relative roles of local and regional processes (e.g., local/regional diversity regressions or randomised null models) are inappropriate for identifying the processes occurring between regional and biogeographic species pools. Nevertheless, the geographical extent of the regional species pool does seem to depend on the biogeographical pool in which it is nested (Box 2) and the next logical step will be to explore why this is so. We suspect that this will require studies exploring the biogeographical variation in local-scale processes (e.g., Jocque et al. 2010, Myers et al. 2013). These data could ultimately unveil how clear biogeographical units emerge from the countless interactions between species at local scales. In addition to these data, macroecologists should develop new theories to link the regional and biogeographic species pools conceptually. However, as we argued earlier, we caution against pursuing this end by modifying existing ecological theories that unify local communities to the regional species pools because ecological processes do not scale in a hierarchical way.

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