Does biogeography need species?

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Abstract

Does biogeography need species? The non–equivalence of species defined using different species concepts has recently been highlighted as a serious impediment for conservation efforts. The question arises then, to what extent biogeographical studies, and especially macroecological studies, might also be hampered by the numerous problems pertaining to multi–species datasets. An examination of what is meant by species across spatial scales reveals an important discontinuity. Over and above the much–debated species concepts the word 'species' describes, in fact, two distinct ideas. One, applicable at the local scale, is critical in a community ecology context. The second refers to non–equivalent units in the global inventory of biodiversity, useful for reference purpose, but problematic where analysis is concerned. The majority of biogeographical studies are in fact relevant to those intermediate spatial scales where neither meaning truly applies. Multi–species lineages that are comparable in one or another respect (such as equal–age lineages and similar–range lineages) are probably more accurate units for testing biogeographical hypotheses.

Key words: Equal–age lineages, Global scale, Higher taxa, Local scale, Range–defined lineages, Species concepts

Resumen

¿La biogeografía necesita especies? Recientemente se ha señalado que la falta de equivalencia de las especies definidas utilizando diferentes conceptos de especie es un grave obstáculo para las iniciativas de conservación. La pregunta que se plantea es hasta qué punto los estudios biogeográficos y, en especial los macroecológicos, podrían verse también perjudicados por los numerosos problemas relacionados con las bases de datos de múltiples especies. Si se analiza lo que se entiende por especie en distintas escalas espaciales se observa una importante falta de uniformidad. Al margen de los conceptos de especie ampliamente debatidos, el término "especie" describe, de hecho, dos ideas diferentes. La primera, aplicable a escala local, es fundamental en el contexto de la ecología comunitaria. La segunda hace referencia a unidades no equivalentes del inventario mundial de biodiversidad, útil con fines de consulta, pero problemática en lo que respecta al análisis. En realidad, la mayor parte de los estudios biogeográficos se realizan en escalas espaciales intermedias, en las que ninguna de las dos ideas es verdaderamente válida. Los linajes de múltiples especies que son comparables en un sentido y otro (como los linajes de la misma edad y los linajes de rango parecido) son unidades probablemente más precisas para comprobar las hipótesis biogeográficas.

Palabras clave: Linajes de la misma edad, Escala mundial, Taxones superiores, Escala local, Linajes definidos por el rango, Conceptos de especie

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Introduction

In the language of ecologists, biogeographers and conservationists alike, 'species' is one of the most commonly used words, topping key word rankings (Kissling et al., 2015; Chytrý et al., 2017), or even being disqualified from such rankings on this very account (Franklin, 2013). However, not everyone using the word 'species' means the same thing, and it is often unclear exactly who means what. A variety of species concepts are employed by taxonomists when defining species and the results of classification efforts based on different concepts can differ widely (Wheeler and Meier, 2000). This is of particular concern to conservation biologists. Regarding the prioritisation of species, an alarm bell has recently been rung (Garnett and Christidis, 2017) calling for some form of standardisation in terms of the species concepts employed. This call is in fact echoing older concerns (Avise and Mitchell, 2007). When prioritising areas rather than species, concern over the use of species–based measures is shown by increasing supplementation with data on phylogenetic relatedness and functional diversity (e.g. Pollock et al., 2017).

Biogeography feeds both data and analysis methods to conservation science, and biogeographers need to stay alert to any concerns raised by conservation scientists as to the validity or reliability of such inputs. Beyond conservation, the theoretical understanding of biogeography depends heavily on what species are understood to be, and on how species concepts are applied. While it has been acknowledged that species need geography (de Queiroz, 2007), it has been considered a given that (bio) geography needs species, and perhaps such a statement needs to be qualified.

The literature on species concepts is substantial (Wheeler and Meier, 2000; Coyne and Orr, 2004; de Queiroz, 2007; Sangster, 2014). The question remains though whether the differences between such concepts actually encapsulate the deepest divide in the discussion over what species (should) mean. It may be useful to take a step back and revisit where the idea of species originates, to what extent contemporary usage is compatible with those initial intentions, and whether those intentions in turn are compatible with the questions contemporary biogeography is aiming to answer. I will attempt this here, before considering whether there are any alternatives to species in biogeographical studies.

A need for order

There is little doubt that humans have a basic and profound need to classify living beings, as with all other things —and that the need to describe life forms as species has its roots in our cognitive processes (Kunz, 2012). Even details such as taxonomic typification (Witteveen, 2015) have clear psychological justifications. If this is the case, one can of course question how real such entities are. The widespread explanation that species have a real existence whe-

reas higher taxa are artificial human constructs is presently being eroded at both ends, with suggestions that neither are species particularly natural (Mischler, 2010; Kunz, 2012; Slater, 2016), nor are e.g. genera substantially more artificial (Humphreys and Linder, 2009; Barraclough and Humphreys, 2015). A recent contribution (Barrowclough et al., 2016) suggests that in fact, at the global scale, subspecies may hold more predictive power than species. Nevertheless, in order for species–based approaches to continue existing for centuries in both their folk and scientific forms, species must presumably have some predictive value (Andersson, 1990).

Species across scales

To understand the origin of the species idea, one needs to refer to the local scale. Among traditional societies, taxonomic knowledge is often detailed, and there is a good match between what scientists and hunter–gatherers perceive as different species within local ecological communities —in the case of both higher plants and tetrapod vertebrates (Berlin, 1992). Those studying biotic assemblages first hand, whether scientifically or otherwise, primarily apply their species concepts at the local scale, where species are represented by populations. Even at this level, morphological and behavioural variation within species exists, but key characteristics of what makes species different (look different, occupy different niches, behave differently, do not interbreed; Chambers, 2012) are seldom contradicted across fine spatial and temporal scales.

Difficulties start to arise when geographic variation kicks in. How broad an area needs to be for variation to be described as 'geographic' is a function of species' ability to disperse and thus keep the gene flow going. In snails or fruit flies, it may be a couple of kilometres (Cowie and Holland, 2008). In some waders or birds of prey, the world is hardly enough (Proches and Ramdhani, 2013). In these well–dispersed groups, there can be substantial gene flow between populations across several or all continents, and sometimes only a couple of isolated islands have populations showing significant morphological discrepancies.

But in most groups, over scales broad enough to result in reduced gene flow, new traits and combinations thereof appear. It is at this point that the issue of delimiting species arises, and with it the matter of employing one or another species concept. Without molecular data, one commonly used guideline is to look at the level of variation that allows two species to co–exist without or with minimal hybridisation, and assume that non–co–occurring populations showing comparable differences are also distinct species (Sangster, 2014). Where molecular methods are employed, decision processes can be similar. Quite often, an important criterion here is reciprocal monophyly, even though a large proportion of all accepted species are in fact paraphyletic (Ross, 2014). Some molecular studies show patterns scarcely

Table 1. Do species concepts make sense when employed at the local and global scale? An evaluation using criteria from Coyne and Orr (2004).

Tabla 1. ¿Tienen sentido los conceptos de especie cuando se utilizan a escala local y mundial? Una evaluación utilizando los criterios de Coyne y Orr (2004).

Criteria (species concepts)	
Local scale	Global scale
Interbreeding (biological species)	
Different species are isolated, with occasional hybridisation. **Yes (almost always)**	Often untestable in nature; many closely related species pairs never meet. Some isolating barriers may not function in the same way across geographic space. **Mostly unknown**
Genetic or phenotypic cohesion (genotypic / cohesion / recognition species)	
Cohesion is maintained within species by interbreeding and same environmental pressures. **Mostly yes**	Levels of cohesion vary with distance; the relevant variables vary in ways which can be continuous or multimodal. **Variable**
Evolutionary cohesion (ecological / evolutionary species)	
Maintained through ecological niche, defined at ecosystem level; essentially species are represented by populations which have clearly described evolutionary trajectories. **Yes (almost always)**	Different populations have different evolutionary trajectories, depending on chance and different local environments. **Mostly not**
Evolutionary history (phylogenetic species)	
A species has a common history, except for occasional in situ speciation events. **Yes (almost always)**	In most species there is a common evolutionary history to the exclusion of all other organisms, albeit a large proportion of all species are paraphyletic. **Mostly yes, but often not**

matching what one sees based on morphology, and the matter of revising species delimitation can then be deferred. Often though, molecular studies result in the description of new cryptic species, that are hard to recognise based on morphology alone. Such descriptions have sometimes been hailed as great victories for conservation, only to be re–assessed soon thereafter (Morrison et al., 2009).

The global species inventory and the northern bias in taxonomy

The species thus described based on morphology and, increasingly, on molecular studies then take their place in a global list of species, which is widely perceived to represent the most reliable measure of global biodiversity, and the estimation of which has become an important topic in itself (Costello et al., 2013). It can be argued, however, that given the lack of uniformity in the methods used, the global number of species represents a better measure of the effort we have put in subdividing biodiversity than a measure of the biodiversity itself. According to most, if not all, major species concepts, it is easier to speak of species at the local scale than globally (table 1). To explain the current global–scale use of species, it may be useful to review some potential biases in research relevant to the use of species.

One such bias is the group of organisms under study. It is certainly easier to speak of species in the case of vertebrates than in the case of plants. It is even more complicated in the case of bacteria, algae or fungi, where reproductive isolation is broken more

Table 2. The logical validity of adding up species to produce values for Whittaker's (1977) levels of biodiversity measurement, with one level added here (global).

Tabla 2. Validez lógica de sumar especies para producir los valores que permitan calcular los niveles de biodiversidad de Whittaker (1977), con un nivel añadido (el mundial).

Diversity level	
'Point' diversity Alpha diversity (local)	Fully valid while noting rare events such as hybridisation or the accidental occurrence of individuals from elsewhere within or even outside region.
Beta diversity (local turnover) 'Pattern' diversity (within beta patterns) Gamma diversity (intermediate)	Largely valid, except for events such as those listed above, and replacement by closely related species in different habitat types. These species pairs do not typically co–occur and their acceptance as different species is down to the species concepts employed.
Delta diversity (within region turnover) Epsilon diversity (regional)	Potentially valid if counting allopatric species pairs/ swarms as single species.
'Global' diversity	Possibly valid in special cases such as taxa with low numbers of species and high species distinctiveness.

often via hybridisation and horizontal transfer of genes (Yakimowski and Rieseberg, 2014; Dudgeon et al., 2017). In most countries and ages, zoological studies have edged botanical ones, not to mention microbiology or mycology, even though animals only represent less than 1 % of the total biomass in most terrestrial ecosystems. This has been attributed to anthropomorphism (Wilson et al., 2007), but being able to delimit species more easily may have also had something to do with it.

Second, geographic intraspecific variation needs time to arise. In places where most animals and plants are recent arrivals, variation is minimal (Hewitt, 2004), and organisms can be easily classified over broader areas. Is it then coincidental that the effort of extrapolating the idea of species from local to global took flight in Linnaeus' post–glacial landscapes of Sweden, and most of world's taxonomists are, to the present day, based in places that used to be under ice at the last glacial maximum? (See patterns in the distribution of taxonomists in Gaston and May, 1992.)

Where do species fit in biogeography?

Biogeography interacts with the idea of species at multiple levels. Most often the very studies defining species include distribution data and as such qualify as biogeography. Analysing these distributions does in fact lend taxonomic and phylogenetic studies a cutting edge, and thus the biogeographical component often takes precedence.

In its macroecological incarnation, biogeography studies multi–species datasets, and more specifically the geographic distributions of multiple species. These are analysed in relation to other variables, either measured for individuals belonging to those putative species (traits such as body size, trophic group, metabolic rate, etc.) or are, as is the case with the geographic range itself, estimated for the species as a whole (age, origin, total abundance). Often, species richness for a given group becomes a variable onto itself, and can be measured at various scales. The broader the scale, the more likely is an operational geographic unit to harbour several closely related allopatric species, meaning the number of species in such a unit depends on taxonomic treatment. A proposed assessment of how valid the use of species is as relevant to the different levels of biodiversity measurement (Whittacker, 1977) is presented in table 2.

Among the variables mentioned above, species richness and geographic range are arguably the most sensitive to potential lumping and splitting exercises. However, functional traits also vary geographically, and the inclusion or exclusion of certain populations may change a species' standing.

A conceptual model of how species usage may have expanded from local to global scale, including some of the biases involved and some potential difficulties, is presented in fig. 1.

Alternatives

Many of the key patterns in biodiversity and biogeography can already be confirmed after discarding species. Barcoding, even though in some ways a black box, is increasingly used as a species–free
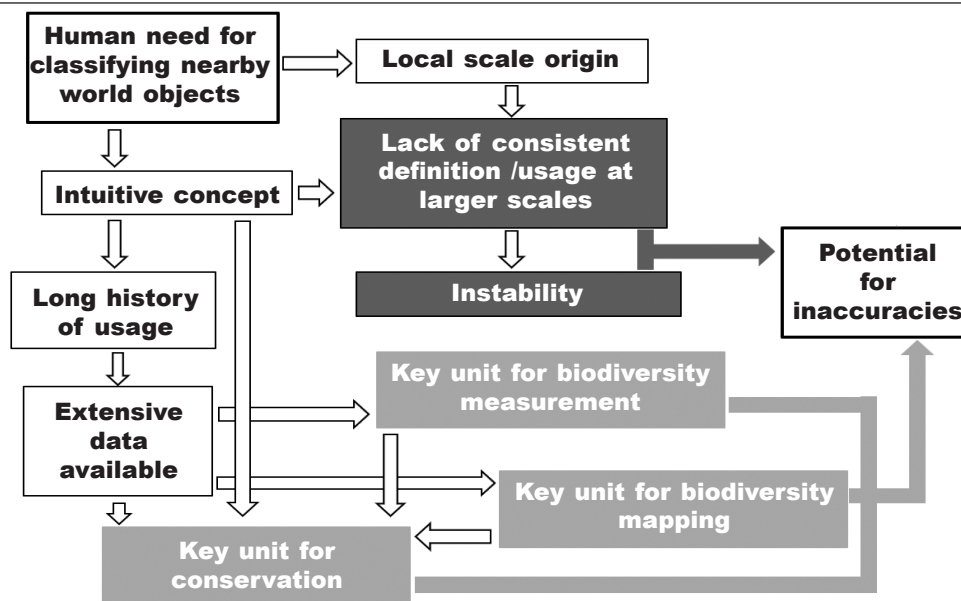
Fig. 1. A conceptual model tracing the species idea from its inception (human need to classify) to the potential inaccuracies plaguing it today (both in bold boxes). The key uses of species–biodiversity measurement and mapping, and conservation prioritisation, in light grey boxes. Dark grey boxes depict the points where problems intervene.

Fig. 1. Modelo conceptual para hacer un seguimiento de la idea de especie desde su concepción (necesidad de los humanos de clasificar) hasta la actualidad, con las posibles inexactitudes que plantea (ambas en cuadros negros). Los principales usos de las especies: medición y cartografía de la biodiversidad y establecimiento de prioridades de conservación se indican en los cuadros gris claro. En los cuadros gris oscuro se indican los puntos problemáticos.

form of biodiversity measurement (Waterton et al., 2013). Species–area curves are paralleled by phylogenetic diversity–area curves —not particularly different except for very fine spatial scales (Procheş et al., 2009; Helmus and Ives, 2012). Species colonisation of islands or new habitats is probably better described as lineage colonisation, and this assists with appreciating the distinction between the number of colonisation events and subsequent diversification. The latitudinal gradient in species richness can be illustrated equally well with multi–species lineages (Davies and Buckley, 2012; Procheş et al., 2015) and with measures of genetic diversity within species (Adams and Hadly, 2012; Araújo and Costa–Pereira, 2013). Simulated genetic and species diversity measures are strongly matched under a variety of modelled scenarios (Vellend, 2005), and this has been tested with real–world data across sites. For example, Cleary et al. (2006) found a 96% match in Bornean butterflies. At broader scales, genetic diversity is also starting to be mapped (Miraldo et al., 2016), and the species–based hotspots of plant diversity have been confirmed using plant phylogenetic diversity, with an 80% match (Daru et al., 2019). In the continuum between allele diversity and the diversity of broad multi–species lineages,

at any spatial scale other than the local community scale, the need for employing species diversity is decreasing.

Insofar as species are road markers to indicate where about in the living world a study is positioned, they are very much still necessary, and the most stringent philosophical approaches questioning the use of species (Stamos, 2004; Kunz, 2012; Slater, 2016) will concede this. Where species become units of analysis, and as such assumed to be somehow equivalent to one another, caution is required. Nevertheless, metrics based on species, and even higher taxa, have been shown to correlate well with arguably more objective measures such as phylogenetic diversity across a variety of studies (e.g. Forest et al., 2007; Pollock et al., 2017). Insofar as species–based metrics remain the easiest to assemble for any given study, one should cautiously employ them —while keeping in mind at all times their shortcomings.

A lineage–based future?

Most patterns and processes relevant to biogeography can be re–examined using sets of multi–species lineages carefully designed for the key questions

Table 3. An outline for using age–based and range–based broad lineages as biodiversity units.

Tabla 3. Resumen para utilizar linajes amplios basados en la edad y el rango como unidades de biodiversidad.

	Age–based broad lineages	Range–based broad lineages
Methodology	Divide phylogenetic tree into all lineages present at a given time in the geological past.	Select from phylogenetic tree lineages at any depth that fit a certain geographic pattern.
Possible variations.	Can include extinct lineages or not.	Can be defined as a % match for a region, biome, realm or whole world.
Biogeographical application	Map the diversity and endemism of such lineages to highlight areas with maximal refugial value since age used to define them (Davies and Buckley, 2012; Procheş et al., 2015).	Map the diversity of such lineages to highlight most representative areas for a region, biome etc., or, map cosmopolitan lineages globally to indicate regions of maximum historical connectivity (Procheş and Ramdhani, 2013).
Macroecological application	Compare lineages of the same age to see how traits affect their survival, distribution, diversity (Procheş et al., 2019).	Compare lineages with similar distribution to understand how traits affect the period of time necessary to achieve that distribution breadth (Procheş and Ramdhani, 2013).
Other potential uses	Suggested for usage in place of taxonomic ranks (older lineages, inclusive of younger ones, in place of higher and lower taxa respectively, Avise and Johns, 1999).	Can be of ecological interest too, as lineages occurring throughout a certain range likely subdivide niche space in a manner that is of regional or global relevance.

of each study. Two of the several possible ways of defining such lineages are detailed in table 3. One of these is equal–age lineages. Their use as taxa was suggested by Henning (as long ago as 1936), resurfaced with the work of Avise and Johns (1999), and is presently taken quite seriously in fungal systematics (Zhao et al., 2016). The idea of mapping them may be rooted in basal versus derived lineage comparisons (Hawkins et al., 2006), and true equal–age lineages were first mapped by Davies and Buckley (2012; 'local lineages through time'). Such maps can illustrate lineage survival from specific age intervals, and provide a picture of refugial value (Procheş et al., 2015; Padayachee and Procheş, 2016) that cannot be encapsulated by phylogenetic diversity, where recent diversifications can add up to match the values derived from ancient lineages (Forest et al., 2007).

For other types of questions, it may be more appropriate to look at equal–range (or at least comparable–range) lineages, from narrow endemic lineages to cosmopolitan ones. Lineage range dynamics has been employed in the understanding of differential survival in refugia (Waldron, 2010), and in the mapping of endemism (Rosauer et al., 2015). Age comparisons for lineages defined based on their range was also used to illustrate the effects of body size and dispersal ability (Procheş and Ramdhani, 2013).

One should keep in mind that lineages are not entirely free from some of the problems that plague species–based approaches. For example, hybridisation and horizontal transfer of genes that happened long ago mean that any phylogeny from which lineages are derived is not a perfect model. Additionally, the same phylogenetic correction methods used for species will be needed to identify or eliminate patterns derived from lineages being more or less closely related to each other.

Nevertheless, lineages present at least two major advantages: they can be made approximately equivalent for the purpose required in a given study, and, if looking at lineages old enough, they come in manageable numbers, meaning one can actually interpret the results with one's own knowledge of biodiversity. Even though the main benefit of using lineages is their equivalence at a scale where species are anything but equivalent, lineages can equally well be used at the local scale (where species do not raise the same

Table 4. A semi–quantitative summary of the data availability, usefulness, feasibility and costs of species in comparison to different lineage types. While current data is certainly best for species, broad lineages are more manageable in terms of number, can be defined quite accurately, and have minimal costs in terms to putting together data sets, as available phylogenies will be in most cases sufficient, especially in the case of age–based lineages. Narrow lineages are numerous, expensive to list (e.g. barcoding) and their definition can vary substantially, but may nevertheless be useful in understanding patterns of plant or animal survival in the geologically recent past, which may be important from a conservation perspective.

Tabla 4. Resumen semicuantitativo de la disponibilidad, la utilidad, la viabilidad y los costos de las especies en comparación con diferentes tipos de linajes. Si bien los datos actuales son sin duda más adecuados para las especies, los linajes amplios son más manejables en cuanto al número, se pueden definir con bastante precisión y conllevan un costo mínimo en lo que se refiere a la compilación de conjuntos de datos, puesto que las filogenias disponibles serán suficientes en la mayoría de los casos, en especial en los linajes basados en la edad. Los linajes reducidos son numerosos, caros de identificar (por ejemplo, mediante el código de barras) y su definición puede variar de forma sustancial, aunque pueden resultar útiles para entender los patrones de supervivencia de plantas y animales en el pasado geológico reciente, lo que puede ser importante desde el punto de vista de la conservación.

	Broad lineages			Narrow leneages
	(age–based)	(range–based)	Species	(species level or below)
Numbers	*	*	****	*****
Definition accuracy	*****	****	***	**
Current data availability	**	*	*****	***
Costs of future data acquisition	*	**	****	*****

problems) if cross–scale analyses are envisaged (Procheş et al., 2019).

Zooming in to a finer phylogenetic scale, within–species lineages have been studied in a variety of ways, and are already contributing a lot to biogeography. Nevertheless, a lot more can be done in terms of finding commonality of patterns. This call, voiced by Hickerson et al. in their 2010 review of phylogeographic research, remains very much relevant today. Searching for such common patterns across lineages may in fact have been more hampered than helped by referring everything to species level. However, one cannot speak of phylogeography and species in one breath, without mentioning speciation. The onset of reproductive isolation in previously cohesive lineages is key to the global accumulation of biodiversity, and this may be the strongest indication that we do need species, and not only to have names for things. This reproductive isolation is highly sensitive to geography. Distance can both increase and decrease the chances of reproductive isolation (Coyne and Orr, 2004; Turelli et al., 2013), and so, at least in that context, biogeography may yet need species after all.

Outlook

The contemporary understanding of global biodiversity cannot be separated from the Darwinian 'tree of life' model. That Darwin chose to call his most influential work 'The origin of species' may therefore seem ironic from a present–day perspective. Where branches of the tree of life co–exist locally, they can certainly be called species in that particular local context. When they do not, their specific status remains a moot point. For conservation purposes, one can call them species, while being aware that, in the global context, a different term should be used. Contemporary biogeography incorporates numerous types of studies, and as such is not bound to a particular range of spatial scales. However, in its most stringent definition it should perhaps refer to that precise interval between the local and the global, where neither meaning of the word 'species' truly applies.

I started this piece by highlighting conservation–related concerns, and it is probably appropriate to end with conservation too. Species distributions alone are not an ideal predictor of an area's conservation value (Araújo and Williams, 2000). Species occurrence in a given place does not mean that the species will be able to sustain itself if conserved there but extirpated in all other places. On the contrary, high within–species genetic diversity is a strong indication that the species indeed has a long history of occurrence there. It is true that environmental change does not always follow the same routine, and anthropogenic change may indeed act very differently from past changes that resulted in the current spatial pattern in genetic variation. Nevertheless, more often than not, documenting high genetic diversity in an area makes it likely that a lineage will also survive there in the future. Similarly, across broader spatial and phylogenetic scales, the occurrence of multiple ancient

lineages in a region is an indication that the region has served as a refugium through geological time. Often this regional–level survival is decoupled from the specifics of the environments where lineages live, with lineages from diverse environments sharing the same regional or global survival patterns. This allows painting a picture of truly global, multi–environment biodiversity hotspots (Forest et al., 2007; Daru et al., 2019; Igea and Tanentzap, 2019).

A lineage focus, whether one refers to narrow genetic lineages or broad multi–species ones, or ideally a combination of the two, is more likely to capture what is needed in conservation than the current species focus, and assembling lineage data sets for this purpose is at least partly achievable (table 4). The word 'lineage' is perhaps ambiguous, and this may have hindered its widespread use in comparative studies, but, as stated here, there is enough ambiguity with 'species' too, even though most conservation–minded people may feel they have an intuitive understanding of what it means. If conservation is to a great extent driven by popular buy–in, and an acceptance of the keywords used is critical, perhaps biogeography can lead an effort to detach itself from a species–centred approach, whether the replacement be lineages, or another.

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