Received: 30 April 2019 | Revised: 25 June 2019 | Accepted: 3 July 2019

DOI: 10.1111/geb.12987

MACROECOLOGY 30TH ANNIVERSARY

Global Ecology and Biogeography A Journal of Macroecology WILEY

The carrying capacity for species richness

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Funding information
Grantová Agentura České Republiky, Grant/Award Number: 16-26369S

Editor: Richard Field

Abstract

The idea that the number of species within an area is limited by a specific capacity of that area to host species is old yet controversial. Here, we show that the concept of carrying capacity for species richness can be as useful as the analogous concept in population biology. Many lines of empirical evidence indicate the existence of limits of species richness, at least at large spatial and phylogenetic scales. However, available evidence does not support the idea of diversity limits based on limited niche space; instead, carrying capacity should be understood as a stable equilibrium of biodiversity dynamics driven by diversity-dependent processes of extinction, speciation and/or colonization. We argue that such stable equilibria exist even if not all resources are used and if increasing species richness increases the ability of a community to use resources. Evaluating the various theoretical approaches to modelling diversity dynamics, we conclude that a fruitful approach for macroecology and biodiversity science is to develop theory that assumes that the key mechanism leading to stable diversity equilibria is the negative diversity dependence of per-species extinction rates, driven by the fact that population sizes of species must decrease with an increasing number of species owing to limited energy availability. The recently proposed equilibrium theory of biodiversity dynamics is an example of such a theory, which predicts that equilibrium species richness (i.e., carrying capacity) is determined by the interplay of the total amount of available resources, the ability of communities to use those resources, environmental stability that affects extinction rates, and the factors that affect speciation and colonization rates. We argue that the diversity equilibria resulting from these biodiversity dynamics are first-order drivers of large-scale biodiversity patterns, such as the latitudinal diversity gradient.

KEYWORDS
biodiversity equilibria, biogeography, diversity dynamics, ecological limits, extinction, latitudinal diversity gradient, macroecology, speciation, species–energy relationship, species richness patterns

1 | INTRODUCTION

During the last few decades, a large effort has been invested into deciphering the causes of large-scale diversity patterns, such as the latitudinal diversity gradient (LDG) (Pontarp et al., 2019). Empirically, it has been shown that species richness is positively related to climate (namely temperature, water availability and the resulting ecosystem productivity; Currie, 1991; Hawkins et al., 2003), area of a region (Rosenzweig, 1995), environmental stability (Jetz & Fine, 2012) and topographical heterogeneity (Davies et al., 2007). The theories put forward to explain these patterns can be distinguished into three major classes (Pontarp et al., 2019). One class comprises theories focused on diversification dynamics as a primary cause of the patterns; the second class focuses on the history of different regions and time available for the accumulation of species; and the third class assumes there are particular region-specific diversity limits determining species richness independently of particular histories of lineage diversification. Although the historical explanations of diversity patterns have become popular during the last two decades (e.g., Kozak & Wiens, 2012; Wiens & Donoghue, 2004), we argue that the third class of explanations, based on diversity limits, receives increasing empirical support, meaning that it is timely to ask what the diversity limits are and whether it makes sense to speak about the carrying capacity for species richness.

This idea is not at all new. Darwin (1859) asked what checks an indefinite increase in the number of species. He suggested that an increase in the number of species for a given amount of resources should decrease population sizes and consequently increase probabilities of extinction, leading to extinction rates rising above rates of species origination and thereby checking diversity from increasing indefinitely. Similar ideas have been developed theoretically by Hutchinson (1959), Rosenzweig (1975) and Wright (1983), resulting in the species–energy theory (Currie et al., 2004) or the more individuals hypothesis (Gaston, 2000), which states that total community abundance limits the number of species with viable populations (reviewed by Storch, Bohdalková, & Okie, 2018). Others have assumed that the number of species is limited by available niche space (i.e., by the total number of potential niches in an environment; e.g., Gavrilets & Vose, 2005). The idea of the carrying capacity of species richness is also implicit in all the theories of diversity dynamics that assume stable equilibria (e.g., Hubbell, 2001). We argue that carrying capacity (whether for population size or for the number of species) should be understood generally as a stable equilibrium of the dynamics rather than a hard limit on the potential maximum population size or number of species, respectively (Box 1). Such a concept of carrying capacity can provide a solid foundation for the development of predictive theory on diversity patterns and dynamics.

Here, we briefly review the evidence for and against the existence of a carrying capacity for species richness. Then, we evaluate potential mechanisms that may set the species richness carrying capacity and show how species richness equilibria are treated in prominent theories of diversity dynamics. We propose an approach that aims to address identified drawbacks of these theories. We highlight the recently developed equilibrium theory of biodiversity dynamics (ETBD; Storch et al., 2018), which provides an example of such an approach. It is a general theoretical framework for species richness carrying capacity that aims to overcome problems previously associated with the concept and provides a consilient approach for understanding first-order causes of macroecological biodiversity patterns.

2 | EVIDENCE OF THE CARRYING CAPACITY FOR SPECIES RICHNESS

Empirical evidence supporting the idea that there are diversity limits or, more precisely, particular equilibria of diversity dynamics that act as attractors of these dynamics (i.e., carrying capacity) have been summarized by Rabosky and Hurlbert (2015), who focused on the evidence of diversity limits of large (continental) biotas. We expand this line of evidence, focusing on: (a) characteristics of observed large-scale spatial diversity patterns, (b) patterns observed in phylogenetic trees combined with information on geographical distribution of taxa, (c) observations concerning contemporary time series showing a balance of species origination and extinction, and (d) palaeontological data. None of these sources of evidence is unequivocal, but together they provide a good basis for considering the carrying capacity of species richness as a vital concept.

2.1 | Large-scale spatial diversity patterns

Species richness patterns are, to a large extent, predictable (Currie, 1991), with the number of species being well correlated with temperature, rainfall or net primary productivity (Field et al., 2009), and diversity patterns for different taxa are largely congruent (Hawkins et al., 2012). This finding cannot necessarily be interpreted only in terms of carrying capacity; humid and hot environments could instead have had higher diversification rates or have been more stable, so that species of various taxa had time to accumulate and adapt to this environment. Indeed, there is evidence for a prevalence of ancient lineages in the tropics (e.g., Duchêne & Cardillo, 2015; Marin et al., 2018; McPeek & Brown, 2007; Pyron & Wiens, 2013; Qian, Jin, & Ricklefs, 2017). However, this pattern cannot be taken as evidence against species richness limits (Hurlbert & Stegen, 2014a), because these limits may themselves drive patterns of rapid diversification or a slow species accumulation (Pontarp & Wiens, 2017). Many recent studies demonstrate that large-scale spatial diversity patterns are largely decoupled of variation in the attributes of diversification histories, such as diversification rate or time since origination; some regions are species rich owing to higher diversification rates (cradles), others owing to the long time for species accumulation (museums) (Belmaker & Jetz, 2015; Davies & Buckley, 2012; Kennedy et al., 2014; Oliveira et al., 2016; Owens et al., 2017). For instance, passerine birds reveal high diversification rates in the Neotropics and low diversification in tropical Australasia, yet they reach comparatively high species richness in both these areas (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). Given that passerines originated in Australasia, the patterns can be interpreted as reflecting a similar high species richness carrying capacity for these areas, which was reached early on in Australasia (leading to diversification rates slowing down to their currently low levels) and relatively recently in the Neotropics, reflected by high diversification rates inferred from phylogenetic trees. Regions with similar species richness and climates thus vary widely in their diversification histories, indicating the existence of attractors of diversity dynamics (i.e., diversity equilibria) and a limited role for historical factors in setting current species richness.

2.2 | The structure of phylogenetic trees

Phylogenetic trees often reveal diversification slowdowns (i.e., decreasing probability of splitting lineages during the course of a

BOX 1 Carrying capacity of populations and the logistic equation

The concept of carrying capacity in population dynamics follows from the logistic equation. However, the equation can be derived in two different ways; we can either assume there is some given abundance limit that affects growth rate when the population size approaches this limit or, alternatively, we can derive the carrying capacity from the idea of density dependence of the growth rate. Here, we argue that the latter way is heuristically superior, because it provides understanding of how carrying capacity emerges from the properties of the dynamics, instead of being assumed a priori as an unspecified limit.

Let us take the standard logistic equation for single population growth. The classical (most common) form of the equation for the rate of change in population size N is as follows:

$$\frac{\mathrm{d}N}{\mathrm{d}t}=rN\left(1-\frac{N}{K}\right), \tag{1}$$

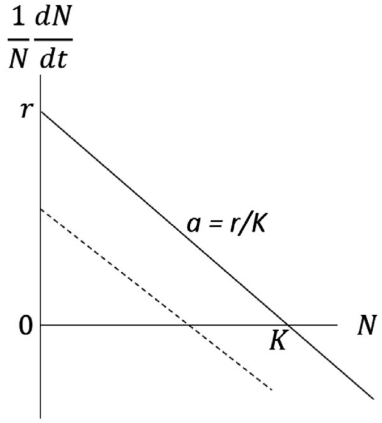
where r is the intrinsic rate of growth and K is the carrying capacity. When written in this way, we implicitly assume that parameters r and K are independent, and K is given a priori, as a level which affects population growth rate if population size approaches this level. However, the logistic equation can be written alternatively (Verhulst, 1838) as follows:

$$\frac{\mathrm{d}N}{\mathrm{d}t}=rN-aN^2, \tag{2}$$

which can be derived by a simple assumption of a linear density dependence of per-capita population growth rate:

$$\frac{1}{N}\frac{\mathrm{d}N}{\mathrm{d}t}=r-aN. \tag{3}$$

The parameter a is the slope of the line relating per-capita population growth to N (i.e., the strength of the density dependence, as shown in the figure below). The density dependence is linear, and if a is viewed as a constant, then the stable equilibrium of the dynamics (i.e., carrying capacity, K) must depend on a and r as $K = r/a$. In other words, if a (the slope of the line) is kept constant, changes in r necessarily lead to changes in K (dashed line).



It can be seen that these two formulations of logistic population growth (Equations 1 and 2) are mathematically equivalent, given that $K = r/a$ (or $a = r/K$). However, the second formulation implicitly considers K as a product of population dynamics (being dependent on the interaction of r and a), and for the constant strength of density dependence a, the K is positively dependent on r (r being per-capita growth rate in the absence of density dependence). There is no a priori reason in either way of reasoning for assuming that the density dependence parameter, a, is determined by given K or, conversely, that K depends on the strength of the density dependence. However, the latter option avoids the so-called Ginsburg's paradox (Gabriel, Saucy, & Bersier, 2005; Ginzburg 1992), in which the addition of a term representing an additional mortality rate [so that $\frac{\mathrm{d}N}{\mathrm{d}t}=rN\left(1-\frac{N}{K}\right)-qN$, where q is the additional per-capita mortality] leads to a stable equilibrium that is no longer equal to K. Also, the second formulation is in accord with empirical and experimental results indicating that selection on increasing r typically also leads to an increase in carrying capacity, in contrast to fundamental assumptions of the theory of r–K life-history trade-offs (Stearns, 1992). The carrying capacity is thus better understood as a consequence of density-dependent population dynamics, rather than vice versa (Gabriel et al., 2005).

Similar reasoning applies to understanding diversity dynamics. Diversity-dependent per-species diversification rate can be written as follows:

$$\frac{1}{S}\frac{\mathrm{d}S}{\mathrm{d}t}=(v-x)-aS, \tag{4}$$

where S is species richness, v is per-species origination rate (speciation plus colonization), x is per-species extinction rate (i.e., $v - x$ is intrinsic per-species diversification rate), and a is the strength of the linear diversity dependence of the diversification rate. The stable equilibrium (i.e., species richness carrying capacity, K_s) is then $K_s=\frac{v-x}{a}$. It thus depends on both the origination and extinction rates. Note that a linear dependence of diversification rate is clearly a large simplification; a somewhat more complex model that includes non-linear diversity dependencies is presented in Box 2.

clade radiation). These slowdowns have been interpreted as a consequence of progressive saturation of ecological space, although alternative explanations exist (Moen & Morlon, 2014). Recently, Machac, Graham, and Storch (2018) have shown that the strength of diversification slowdown in mammalian clades is related to the overlap of species ranges within clades, so that clades with many overlapping ranges reveal more pronounced slowdowns. Although this does not provide a direct demonstration of the existence of diversity limits or equilibrium states, it indicates progressive saturation by species owing to interspecific competition. Likewise, Kennedy et al. (2018) have shown that diversification slowdown in bird clades is related to species range overlap, and the clades not revealing slowdown are those that expand geographically or in functional space.

The interpretation of phylogenetic patterns can sometimes be tricky, because the signal of diversification history may not always be present in phylogenetic trees based on contemporary species; even equilibrium diversity dynamics may produce phylogenetic trees without a signature of slowdowns (Hurlbert & Stegen, 2014a, 2014b). The lineage-through-time plot of bird diversification, for instance, seems to indicate a continuous increase of species richness (Jetz et al., 2012). However, the diversification rate of modern birds (Neoaves) after the mass extinction at the Cretaceous–Tertiary was much larger than would be sustainable in the long term: In the first 15 Myr, 32 independent lineages emerged, whose descendants have survived until now (Jarvis et al., 2014). If the radiation continued with the same speed, there would be > 8,000,000 bird species today, almost 1,000 times more than the 10,000 extant bird species today. This indicates that the ecological opportunities that emerged after the mass extinction largely disappeared, slowing down subsequent diversification considerably. Generally, although the advocates of non-equilibrium diversity dynamics (e.g., Harmon & Harrison, 2015) often stress the fact that diversity sometimes increases rapidly, without apparent bounds, such rapid increases of diversity typically follow periods of mass extinction (Alroy, 2010; Krug & Jablonski, 2012); i.e., in periods when diversity is far below the carrying capacity.

2.3 | Community time series

Many communities reveal approximately stable species richness regardless of significant species turnover (Brown, Ernest, Parody, & Haskell, 2001; Gotelli et al., 2017), i.e., regardless of abundant species extinction and origination events. This observation motivated the development of the equilibrium theory of island biogeography (ETIB; MacArthur & Wilson, 1963, 1967). In some cases, as in the ETIB, the stability of species richness simply reflects a relatively constant species pool; colonization rate is negatively dependent on local diversity, because if there are many species from a species pool at a given site, the probability of occurrence of new species decreases. Although this leads to equilibrium diversity dynamics, it cannot be taken as general evidence of species richness carrying capacity, because in this case it is a by-product of a given (and constant) species pool size.

More interesting are the cases when the apparent stability in species richness is not driven by stability of the source pool of species, e.g., on oceanic islands, where colonization from a stable species pool is not a dominant process, and in-situ speciation plays a role. Sax, Gaines, and Brown (2002), for instance, have shown for birds that the total number of naturalized exotic species on oceanic islands is approximately equal to the number of species that recently went extinct, indicating a carrying capacity for species richness. In contrast, this does not apply for plants, where the number of new species exceeds the number of extinctions of native species. The authors interpret this as a non-equilibrium situation, so that the species richness of plants exceeds the carrying capacity, but the process of extinction in plants is slow and would probably reach the equilibrium after many decades (Sax et al., 2002). Although this might not necessarily be the case, this idea illustrates that the concept of diversity equilibria may be useful even in apparently non-equilibrium situations. Many communities do not reveal stable species richness in the long term, but these cases can be interpreted as reflecting either changes in the equilibrium value (i.e., carrying capacity) or some fluctuations around equilibria, rather than undermining an important role for species richness carrying capacity.

2.4 | Fossil time series

Palaeontological data are notoriously fragmented and incomplete; therefore, making inferences on diversity dynamics at the scale of thousands to millions of years is difficult. This is exemplified by the large discordance between the curves describing temporal variation of marine fossil diversity (measured using the number of genera or families) during the Phanerozoic (e.g., Alroy et al., 2008; Sepkoski, Bambach, Raup, & Valentine, 1981). Some of these curves reveal relative stability during the Palaeozoic, followed by near-exponential increases in the number of genera after the end-Permian extinction (Benton & Emerson, 2007). However, there are methodological problems associated with the "Pull of the Recent" (Foote, 2000), and the curves that avoid this problem do not indicate a continuous increase of species richness but instead relatively wide fluctuations in diversity levels during the whole Phanaerozoic (Alroy, 2010; Alroy et al., 2008). Nonetheless, diversity fluctuates within some bounds, relative to the potential of diversity dynamics; assuming that speciation happens once in 4 Myr (which is a conservative estimate), each evolutionary lineage would have the potential to generate four billion species since the end-Permian extinction, if there was no negative diversity dependence of diversification dynamics.

A line of evidence of negative diversity dependence of diversity dynamics stems from global marine data (Alroy, 2010) and from more detailed regional palaeontological data. Alroy (2009) has shown that fluctuations in the diversity of North American fossil mammals are much smaller than predicted by a model in which observed species origination and extinction rates are randomly assigned to individual time intervals, and Brodie (2019) demonstrated the diversity dependence of Cenozoic mammal diversity dynamics. Additionally, there is increasing evidence that diversification in one group of mammals suppresses diversity in another group (Silvestro, Antonelli, Salamin, & Quental, 2015).

In summary, although there is debate on some of the details of diversity dynamics in fossil time series, there is compelling evidence indicating that diversity dynamics in the fossil record are diversity dependent and fluctuate within some bounds, even though these bounds may be relatively wide.

3 | WHAT SETS THE CARRYING CAPACITY FOR SPECIES RICHNESS?

There are several possible factors and mechanisms that can potentially limit an unbounded increase in species richness. Models of niche filling (Gavrilets & Vose, 2005), for instance, develop an intuition that the increasing number of species fills the available niche space, making it increasingly difficult to find new niches (Price et al., 2014). Although intuitively appealing, the idea that species richness is limited only by available niches has several problems. Niche space is, by definition, multidimensional, and the number of dimensions and the total niche volume may change with species richness, meaning that ecological space filling (niche packing) is not a necessary consequence of increasing species richness (Pellissier, Barnagaud, Kissling, Sekercioglu, & Svenning, 2018). Also, species may have the capacity to divide niche space almost infinitely finely (Rosenzweig, 1995) or to coexist with nearly identical overlapping niches (Hubbell, 2001), meaning that higher species richness simply leads to narrower or more overlapping niches. Also, the idea that niche space directly limits diversity does not have strong empirical support: many resources often appear unsed within communities (Lawton, 1982), and used niche space (measured, for instance using species traits) has been found to be correlated only weakly with species richness (Šímová et al., 2015). In fact, there is substantial ecological theory dealing with these issues, including the theory of limiting similarity (Abrams, 1983; MacArthur & Levins, 1967) and the coexistence theory (Adler, HilleRisLambers, & Levine, 2007; Chesson, 2000; Hubbell, 2001), which suggest that a simple view that the number of species is limited only by available niche space is misleading.

It is thus more reasonable to consider the carrying capacity to be a stable dynamic equilibrium reflecting the balance of extinction, colonization and/or speciation, and assuming that at least one of the processes is diversity dependent. Such a view does not exclude a role for niches in affecting diversity by modulating origination and extinction processes. In such a view, the carrying capacity itself depends on parameters of the processes, and thus equilibrium species richness does not represent a hard limit to the number of species supported by an environment but instead depends on speciation, colonization and extinction rates (Figure 1). In this respect, it is conceptually very similar to the concept of carrying capacity for populations, which also represents the stable equilibrium of density-dependent population dynamics (Box 1), emerging by a balance between rates of natality, mortality, immigration and emigration.

In principle, a stable diversity equilibrium (i.e., carrying capacity) may be driven by the diversity dependence of any of the three processes (colonization, speciation or extinction). Colonization for a local community is certainly diversity dependent in the case of a stable species pool (see section 2.3 above). However, colonization rate is progressively less relevant when moving up towards larger spatial scales (i.e. towards regional species richness), determined mostly by the balance of speciation and extinction (Rosenzweig, 1995). Both these rates may be diversity dependent via the negative effect of species richness on population sizes (assuming approximately constant abundance or inflow of resources, as explained above). However, although diversity-dependent speciation has been assumed by some authors (e.g., Rabosky, 2013), there is no consensus concerning the effect of population size on the probability of speciation (Dynesius & Jansson, 2013; Lanfear, Kokko, & Eyre-Walker, 2014; Orr & Orr, 1996). It is probable that the effect differs between taxa and regions according to differences in the prevailing speciation mode, spatial structure of populations and geographical factors, and thus speciation rate cannot be treated as always being negatively diversity dependent. From a macroecological perspective, it is therefore more reasonable to assume that the diversity dependence of diversification dynamics follows from the diversity-dependence and consequently population size-dependence of extinction rates, whose universality is well established (Ovaskainen & Meerson, 2010). Owing to ultimately limited energy availability, populations become smaller when species richness increases, thus increasing extinction rates regardless of the exact structure of niche space.

4 | ARGUMENTS AGAINST THE IDEA OF A SPECIES RICHNESS CARRYING CAPACITY

The idea that each region has a capacity for maintaining a particular species richness has been widely discussed (Cornell, 2013; Rabosky & Hurlbert, 2015; Wiens, 2011). Several arguments have been put forward against the existence of a carrying capacity for species richness (Harmon & Harrison, 2015). Here, we suggest that these arguments mostly stem from too narrow understanding of the concept of carrying capacity (Box 1). Specifically, the concept becomes problematic when it is assumed that it is an upper limit to the number of species supported by an environment. In contrast, when it is understood as a stable equilibrium of diversity-dependent dynamics of species richness, the problems disappear. Below, we discuss the major arguments in the light of considering species richness carrying capacity as a stable equilibrium of biodiversity dynamics.

1. Communities are open; it is often possible to add new species without affecting the number of native species, as indicated by invasion patterns (Sax et al., 2002). These patterns do not violate the existence of carrying capacity, because diversity need not be exactly in equilibrium at all times, just as population sizes may fluctuate widely around population carrying capacity. An addition of species may temporarily elevate species richness, but

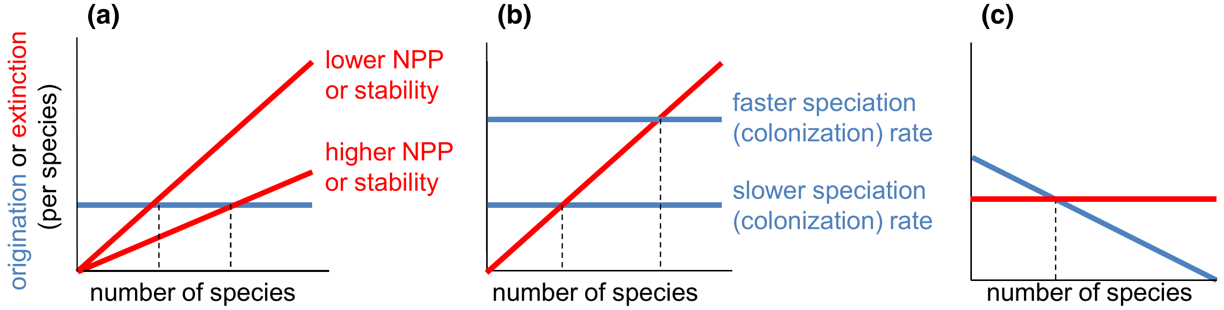


FIGURE 1 The basic idea of equilibrium diversity dynamics can be depicted graphically using curves that relate community-wide origination (= speciation and/or colonization; blue) and extinction (red) rates. For a given amount of resources, per-species extinction rate increases with increasing species richness, because it leads on average to smaller populations more prone to extinction. (a) The slope of the extinction function can depend on environmental factors, such as total productivity [net primary productivity (NPP)] or environmental stability, and resulting equilibrium species richness (dashed lines) is given by the intersection of the extinction and origination function. (b) Equilibrium richness is higher if (for any reason) the origination rate is higher; its level thus depends on rates rather than being directly dependent on some a priori given number of niches. (c) The origination curve can decrease with species richness, as in the case of the equilibrium theory of island biogeography (ETIB), in which the probability of colonization decreases with the number of species already on the island. The ETIB thus does not rely on an assumption of increasing per-species extinction rate with increasing species richness (owing to decreasing mean population size), although the original formulation of the ETIB (MacArthur & Wilson, 1963) assumes this positive diversity dependence of per-species extinction probability. Potentially, origination probability may even increase with the number of species (e.g., when "diversity begets diversity"). Nonetheless, the equilibrium exists whenever both curves are constant in time (or at least fluctuating around an attractor), and it is stable whenever the extinction curve has a higher slope than the origination curve. Note that although these plots are heuristically useful, the parameterization of the curves is problematic, so that these ideas can hardly be used for quantitative predictions [Colour figure can be viewed at wileyonlinelibrary.com]

if the extinction rates owing to lower availability of resources are higher than the origination rates, species richness will have a tendency to decrease back to an equilibrium level. This may take a long time, especially in long-living and/or sedentary taxa, such as plants (Sax et al., 2002). Moreover, a continuous increase of colonization rate would lead to an increase in the equilibrium diversity value (Figure 1), so that the observed increases in the number of species owing to biological invasions might reflect a new equilibrium owing to elevated colonization rates, not necessarily a deviation from an equilibrium.

2. Local community diversity does not exhibit a systematically positive relationship to productivity (Adler et al., 2011; Mittelbach et al., 2001; Šímová et al., 2011), and large-scale diversity patterns are often related to region-specific diversification rates or region age. Given that carrying capacity is a stable equilibrium of species richness, it does not reflect only resource abundance or productivity that mediate diversity-dependent extinction rates, but also the other factors affecting diversity, namely the rates of speciation, colonization and extinction. High variation in the productivity–diversity relationship at small scales may be attributable to problems with productivity measurements (Šímová & Storch, 2017) or to the multitude of factors participating in the relationship (Šímová, Li, & Storch, 2013). In general, given that diversity equilibria are driven by factors affecting extinction and origination rates, ecosystem productivity is not expected universally to be the strongest driver of species richness, although it is often a good correlate of diversity and is expected to affect diversity equilibria through its effect on population sizes (Storch et al., 2018).
3. Niche space is unsaturated. There is a long history of studying community saturation and the utilization of resources (e.g., Lawton, 1982, Cornell, 1993). Taken together, these studies indicate that resources are often unused, and local community richness is often largely a reflection of the richness of the regional species pool. In other words, many local communities host a considerably lower number of species than they would if their species pool were larger. These observations would violate the idea of species richness carrying capacity only if it were understood as a saturated niche space or hard ecological limit rather than a stable dynamic equilibrium. Indeed, local species richness is given by the interplay of colonization and extinction, and larger species pools lead to higher probabilities that species colonize local communities, thus increasing local richness. Species present in a community may not be able to use all of the niche space, but species richness may still be in stable equilibrium (Walker & Valentine, 1984). New species may find ways to use new resources, but as species richness increases, this may be progressively more difficult, so that in a given moment the extinction rate is balanced by the origination rate, and equilibrium is attained.

5 | THEORIES OF EQUILIBRIUM DIVERSITY DYNAMICS

Several formal theories have been proposed to model equilibrium diversity dynamics. One class of models assumes community-wide (or region-wide) rates of species origination and extinction, with some of the rates being dependent on species richness (e.g., Rosenzweig, 1975; Triantis, Economo, Guilhaumon, & Ricklefs, 2015; see Figure 1). This approach provides a heuristic tool to understand how species richness carrying capacity emerges via the balance of diversity-dependent rates but is crucially dependent on our ability to construct respective curves, which is extremely difficult without specific assumptions that are necessarily based only loosely on an ecological theory. One possible simplification comprises an assumption that all the curves depicting relationships between species richness and respective rates may be approximated as power laws (e.g., Triantis et al., 2015) to infer predictions concerning species richness (Box 2).

Another option is to model the dynamics explicitly, using a set of simple rules, well founded by an ecological theory (Rosindell, Harmon, & Etienne, 2015). The neutral theory (Hubbell, 2001) is an excellent example of such an approach. Diversity dynamics are modelled using an individual-based approach, in which all individuals have equal probabilities of birth, death, migration and speciation. The process leads to an equilibrium species richness driven by a diversity dependence of extinction rates; given that the total number of individuals is assumed to be constant, increasing species richness leads to smaller populations of individual species and higher per-species extinction rates (extinction is attributable to community drift in this model, whose speed is negatively related to abundance). Diversity is thus regulated by a limit on the total number of individuals (across all species) and, in this respect, it is in accord with the more-individuals hypothesis (MIH; Gaston, 2000), which states that the number of species is determined by the total number of individuals. However, the MIH has been only vaguely formulated and does not consider other processes affecting the dynamics and, consequently, equilibrium diversity (Storch et al., 2018). A proper theory of diversity dynamics has to consider these effects simultaneously with the effect of resource (and total abundance) limitation, and neutral theory is an example of such a theory, in which equilibrium species richness is determined by total community abundance, speciation rate and dispersal rate (Hubbell, 2001). An extension of neutral theory that

BOX 2 A minimal model of regional diversity dynamics

Let us assume that at large (regional) spatial scales, the variation in colonization rate plays a negligible role in comparison to speciation and extinction rates in determining diversity dynamics. Thus, diversity dynamics may be modelled using assumptions on the whole-community rates of speciation and extinction, with both these rates being dependent on standing species richness via its effect on mean population size, J/S, where J is total community abundance and S is species richness. These dependences can be approximated by many functions. A useful approach is the approximation by power laws, which comprise both increasing and decreasing functions with varying curvature characterized by two parameters (in the log–log scale expressed as slopes and intercepts of the lines). We can assume that per-species speciation and extinction rates depend on mean population size as $v\left(\frac{J}{S}\right)^q$ and $x\left(\frac{J}{S}\right)^z$, respectively, where v and x are the scale factors, which are parameters setting the overall levels of speciation and extinction rates, respectively (intercepts in the log–log expressions of the power laws), and q and z determine the strength of the dependence of speciation and extinction on mean population size (the curvature of the function in arithmetic space). We assume here that q is either equal to zero or is positive (speciation rate is either roughly independent of mean population size or increases with population size, as assumed in the neutral theory of biodiversity), and z is negative (extinction rate decreases with mean population size). Then, the diversity dynamics is given by the difference between total speciation and total extinction rate, such that:

$$\frac{\mathrm{d}S}{\mathrm{d}t} = Sv\left(\frac{J}{S}\right)^q - Sx\left(\frac{J}{S}\right)^z. \tag{5}$$

Equilibrium species richness (K_s) is then:

$$K_s = J\left(\frac{v}{x}\right)^{\frac{1}{q-z}}. \tag{6}$$

This means that large-scale equilibrium species richness is predicted (everything else being equal) to be proportional to total community abundance, J, and depends positively on the ratio of the speciation and extinction parameters, v and x (which can, for instance, reflect topographic heterogeneity and environmental instability, respectively). Additionally, we can confidently assume that $x > v$, because $v > x$ would unreasonably imply that species have higher probabilities of extinction than speciation in communities with very low richness and large population sizes. Thus, given that $x > v$, equilibirum richness is expected to be dependent positively on the difference between the "curvature" parameters, q and z. This implies, for instance, that equilibrium species richness would be proportional to per-species speciation rate if the speciation rate was independent of mean population size (i.e., $q = 0$) and if the extinction rate was, at the same time, inversely proportional to the mean population size (i.e., $z = -1$), which are the simplest assumptions. A downside of this minimalist model, however, is that it addresses only the whole-community rates of origination and extinction. It may be more fruitful to develop theory that assumes that species differ in their abundances and to addresses how the probability or rate of speciation and extinction of an individual species depends on population size, in addition to how population sizes are affected by total energy availability and species richness. This is addressed by the equilibrium theory of biodiversity dynamics described in the main text.

geographically varies the number of individuals and temperature (presumingly, affecting speciation rate) can produce relatively realistic large-scale patterns of species richness on land and in the oceans (Worm & Tittensor, 2018).

However, even though the neutral theory (including its extensions) is able to predict several macroecological/biodiversity patterns, it has several problems and should not be treated as a universal theory of equilibrium biodiversity dynamics. The assumption that individuals of all species are demographically equivalent and have equal access to all resources is too restrictive and biologically unrealistic for most species assemblages that comprise species differing in their niches and habitat/resource preferences. A more general problem concerning the majority of current equilibrium models of biodiversity dynamics is that the diversity limits (or, more precisely, stable equilibria) are assumed to follow from hard limits on the total number of individuals in a given system. But the total number of individuals is not a value that is determined directly by an environment; instead, it is an emergent property of a community, resulting from many species-level dynamics (Storch et al., 2018). It is reasonable to assume that a higher number of species is able to use resources better, meaning that the addition of species (either by speciation or by colonization) opens new possibilities for resource use and thus increases the total community abundance. However, even in such a case there can be a stable equilibrium of species richness if the resources are ultimately limited (e.g., by total energy flow into given system), so that the opportunities to use new resources disappear progressively with the increasing number of species (Storch et al., 2018). The equilibrium species richness will then depend not only on the total amount of resources (or energy availability) and the origination and extinction rates, but also on how strongly changes in species richness affect resource utilization.

6 | A GENERAL EQUILIBRIUM THEORY OF BIODIVERSITY DYNAMICS

The considerations above are addressed by the recently proposed equilibrium theory of biodiversity dynamics (Storch et al., 2018). The ETBD is a species-based theory, representing a middle ground between overly coarse community-wide theories (Box 2) and overly restrictive individual-based models. It predicts equilibrium species richness at regional scales determined by the interplay between speciation, extinction and the availability and utilization of resources by communities. It assumes that species within a region have different abundances, following a particular species abundance distribution (SAD; Box 3), and their probabilities of speciation (i.e., producing a new species) and extinction are functions of these population sizes and of a variety of environmental factors (e.g., isolation and temperature affect speciation rates, and environmental stability affects extinction rates). During a given time interval, some species go extinct and some speciate (Figure 2). Owing to constraints of species in their potential to use resources, some resources may remain unused; however, this amount decreases with an increasing number of species due to the concomitant addition of species traits and abilities that lead to new ways of resource utilization.

BOX 3 Incorporating the species abundance distribution into the theory of biodiversity dynamics

In order to develop a theory of biodiversity dynamics that addresses the effects of population size on rates of extinction and speciation, the shape of the species abundance distribution (SAD) must be either derived or assumed a priori. In the equilibrium theory of biodiversity dynamics (ETBD), which adopts a relatively coarse-grained approach, the SAD is an input of the theory and is assumed to be relatively invariant (i.e., independent of particular speciation and extinction events). Such an assumption is supported by evidence that the overall shape of the SAD is robust and universally characterized by the prevalence of rare species (McGill et al., 2007) or, to be precise, by a relatively regular distribution of abundances across logarithmic classes, meaning that a few most abundant species have abundances several orders of magnitude higher than the majority of other species. The rationale for assuming the SAD as an external input of the ETBD instead of taking the SAD as a product of the dynamics is based on the empirical and theoretical evidence that the SAD is an output of many interacting processes instead of being universally dominated by a single process addressed by a single mechanistic model (Pueyo, 2006; Pueyo, He, & Zilio, 2007). Indeed, niche differences can play a role in addition to spatial (meta)population dynamics; therefore, it would be inappropriate to model the SAD as a result of a narrowly defined process.

Generally, there are two typical strategies to developing macroecological models and theory. One approach is to build a comprehensive model that includes all the processes considered important and to derive all the patterns from it. Such models must either err on the side of extreme simplicity (ignoring key ecological processes and patterns in order to model an idealized system, as is the case of the neutral theory) or have many parameters that are difficult to evaluate empirically. An alternative modelling strategy is to use relatively independent building blocks, whose reliability has good empirical or theoretical foundation, so that the theory comprises a combination of these building blocks. The advantage of this latter strategy, which we have adopted in ETBD (Storch et al., 2018), is that the resulting theory is not dependent on the peculiarities and exact setting of individual processes and can be modified to accommodate changes in the empirical bases for the individual building blocks. Such a theory can then either be formulated generally or be specified in several ways to explore predictions under differing assumptions.

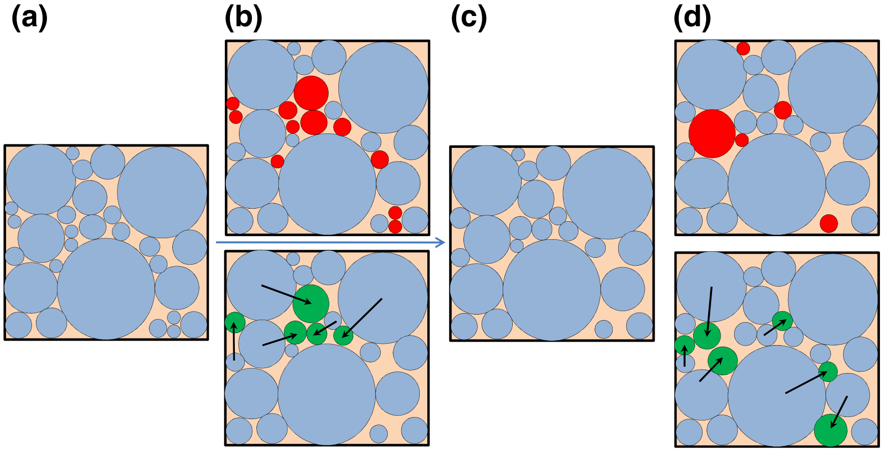


FIGURE 2 The basic idea of the equilibrium theory of biodiversity dynamics. The area of the squares represents the total energy availability of a given region translated into maximum community size in terms of the total number of individuals across all species (note that we do not assume any particular niche structure, thus the spatial positioning within the squares is irrelevant). (a,b) Individual species, depicted by circles whose size represents abundance (a), may go extinct (red circles) or speciate (new species are green, and their origination from ancestral species is indicated by arrows) (b). If the species richness in the new community is lower than the equilibrium value (c), there are more unused resources and/or species have on average higher abundances, meaning that later there are fewer extinctions and/or more speciations (and vice versa) (d). Note that some resources always remain unused owing to various constraints, which is represented in this figure by the fact that a finite number of non-overlapping circles can never fully cover a plane [Colour figure can be viewed at wileyonlinelibrary.com]

Under constant total resource availability, an increasing number of species naturally leads to an increasing proportion of species with small population sizes (Figure 2). A stable equilibrium of species richness appears if the functions relating extinction and speciation probability to population size do not change substantially through time and intersect each other so that net diversification (i.e., speciation minus extinction) increases with population size. There is solid support for these baseline assumptions, because population size universally has a negative effect on extinction probability but no known consistent and universal effect on speciation probability owing to the variety of complex geographical, genetic and taxon-specific factors affecting speciation. Speciation probability is thus likely to be roughly invariant or, if anything, increases with population size (e.g., as assumed in the neutral theory). Equilibrium diversity is then determined by: (a) the functions that relate speciation and extinction rates to population size, i.e., the parameters that affect the overall rates (related, e.g., to geographical isolation and environmental fluctuations, respectively) as well as the strength of the diversity-dependence; (b) the shape of the SAD; and (c) the function determining how species richness and the resource supply (or energy influx) affect the total number of individuals (which, in combination with the SAD and number of species, determines abundances of individual species).

The framework formulated in this way is very general and addresses the core elements of previous attempts to model large-scale equilibrium diversity dynamics. Despite this generality, it provides testable macroecological predictions of species richness patterns, based on two fundamental phenomena that seem to be universal and, at the same time, neglected by most current theories.

First, it pinpoints the population size dependence of extinction rate as the universal mechanism responsible for the diversity dependence and thus equilibrium dynamics, because although speciation rate may also be diversity dependent, the speciation functions are probably very idiosyncratic and taxon specific. The ETBD thus shows that universal (i.e., macroecological) patterns emerge from the universality of the extinction process and extinction dependences. Additionally, it explicitly states that extinction probability depends on population size and population fluctuations (Ovaskainen & Meerson, 2010), meaning that equilibrium richness is affected simultaneously by resource abundance and the fluctuations of resources or environmental conditions. Species richness is thus expected to increase with the total amount of resources and with their temporal stability (Toszogyova & Storch, 2019).

Second, the ETBD assumes that, all else being equal, the level of resource utilization (and thus total community abundance and/or biomass) increases with increasing species richness, although necessarily in a decelerating rate in species-rich communities, given that resources are ultimately limited. The relationships between energy/resource availability, total community abundance and species richness are thus more complex than in theories assuming that community abundance is given a priori. Specifically, the relationships between productivity and species richness and those between community abundance and species richness are predicted to vary between regions with different overall levels of extinction and speciation rates. Regions with lower speciation and/or higher extinction rates (e.g., those characterized by low topographic heterogeneity, low temperature and/or higher resource fluctuations) are predicted to be undersaturated in species richness relative to the productivity level and, consequently, have lower total community size and a lower capacity to use available resources (Storch et al., 2018). Another consequence of the assumption that species richness affects the level of resource utilization is that at comparable levels of ecosystem productivity, higher species richness leads to higher total community abundance and/or biomass, but at a progressively decelerating rate, so that higher species richness is typically not associated with a proportionally higher total abundance.

Another set of predictions of the ETBD comprises different equilibrium diversity patterns along gradients of temperature and productivity, and between ectotherms and endotherms. Given that in ectotherms, metabolism and consumption rate increase with increasing temperature, their maximum community abundance is predicted to decrease with increasing temperature for a given amount of resources, affecting species' population sizes, extinction rates and species richness. In contrast, speciation rates are predicted to increase with temperature in ectotherms (Allen, Gillooly, Savage, & Brown, 2006), which, for a given level of resource availability, potentially increases species richness but decreases species abundances. The resulting patterns will depend on the degree to which temperature and total resource availability covary along environmental gradients. In contrast, patterns in endotherms are expected to be driven by environmental temperature only indirectly, via the typically positive effect of temperature on primary productivity.

The exact quantitative predictions of these relationships depend on the exact parameterization of respective processes. All these predictions, and the assumptions, require further testing to evaluate whether the ETBD can be treated as a general macroecological theory of diversity dynamics.

7 | DISCUSSION

Some authors have argued that the idea of species richness limits or carrying capacity for species richness has been abandoned rightfully, as a result of the accumulation of evidence that seriously challenged it (Harmon & Harrison, 2015). Such a statement is justified only when the concept of carrying capacity is taken very narrowly, e.g., when carrying capacity is understood as reflecting a fully saturated niche space that does not allow addition of other species. However, we have argued that denying an important role for species richness carrying capacity is inappropriate when carrying capacity is considered as an equilibrium value that is affected by diversity-dependent rates of species origination and extinction, analogous to how population carrying capacity results from density-dependent natality and/or mortality.

There are three possible statements concerning species richness carrying capacity, differing in their generality and validity. The first one is that there are stable equilibria of diversity dynamics. Such a statement is trivial and almost tautological. Any dynamical system has its equilibrium points, some of them being stable (in the sense that a small deviation from this point leads back to the equilibrium). Some of the stable equilibria are uninteresting (e.g., when there are no species), but there must also exist non-trivial stable equilibria at high species richness, given simply by the fact that the maximum number of all individuals in a community, or maximum total biomass, is limited by space, energy availability or other physical settings. If species richness were too high, almost all species would have such small populations that they would go extinct at a faster pace than any feasible origination rate (Darwin, 1859), lowering richness back to its equilibrium value. Even when these equilibria exist, richness may still exhibit completely non-equilibrial dynamics if species richness is far from such equilibria for its entire history. Also, the equilibrium values (technically, its parameters) may change more quickly than species richness itself (i.e., than the processes of speciation, colonization and extinction; Quental & Marshall, 2013). In such a case, the carrying capacity would also never be attained even though it exists as an ever-changing attractor of the dynamics.

The second possible statement is that regionally different diversity equilibria are responsible for macroecological biodiversity patterns (Rabosky & Hurlbert, 2015). In contrast to the previous formulation, it is an empirical statement, a hypothesis that should be (and has been) tested. We have shown that this statement has considerable empirical support. During the last few years, evidence has accumulated that species richness patterns cannot be attributed simply to species accumulation times or diversification rates; instead, they converge to mutually consistent patterns unrelated to diversification dynamics (Belmaker & Jetz, 2015; Kennedy et al., 2014; Oliveira et al., 2016; Owens et al., 2017), probably reflecting different carrying capacities (i.e., diversity equilibria). Also, evidence of ecological causes of diversification slowdowns (Machac et al., 2018) indicates that species richness cannot increase without limits, and these limits seem to be region specific. The ETBD shows that these regional diversity equilibria may emerge from the interplay of diversity-dependent extinction and speciation rates modulated by energy availability, environmental stability, temperature and topography.

The third and strongest statement would be that in most species assemblages, species richness is in equilibrium (i.e., very close to its carrying capacity). Stated in this way, it is almost certainly wrong. Disturbances often push diversity away from equilibria, although frequent and regular disturbances can be interpreted as elevated extinction rate affecting the equilibrium species richness level (similar to population dynamics, in which occasional disturbances may be understood as elevated mortality, affecting r, and thus also K; see Box 1). Additionally, it may be possible for species richness to exhibit similar oscillatory behaviour around an equilibrium value to those predicted for populations and other nonlinear systems. Regardless, carrying capacity is a useful concept even when an ecological system is largely non-equilibrial, because it is hard to refer to and gauge a non-equilibrium state without an idea of an (ideal, and possibly unattainable) equilibrium. And whether the world is considered equilibrial or non-equilibrial is largely a matter of scale; the concept of carrying capacity is useful when the parameters of the dynamics do not change too fast, so that the fluctuations of diversity around the equilibrium value are faster and more frequent than changes in the equilibrium level itself. Consequently, it makes sense to speak about diversity equilibria only at the phylogenetic scales (Graham, Storch, & Machac, 2018) at which the key parameters are relatively stable, namely only for species richness of a large taxonomic group whose total resource availability does not change too much. Diversity dynamics of smaller clades are probably affected by continually changing diversity in other competing clades (Silvestro et al., 2015), leading to rapid changes in parameters of the dynamics. Therefore, it makes more sense to speak about species richness carrying capacity at phylogenetic scales that encompass multiple interacting groups (e.g., whole orders or classes of vertebrates; Machac et al., 2018). The evaluation of this phylogenetic scale-dependent diversity dynamics is a crucial next step in this endeavour (Graham et al., 2018).

The concept of species richness carrying capacity (i.e., diversity equilibria) has profound consequences for understanding current changes in biodiversity. In fact, some key concepts, such as extinction debt, do not even make sense without assuming that diversity equilibria exist; extinction debt means that species richness is due to habitat loss in disequilibrium and will ultimately reach a lower equilibrium level given by habitat area. Generally, any diversity anomalies are hardly interpretable without referring to some expected equilibrium number. Even more importantly, if diversity (at least at some spatial, temporal and phylogenetic scales) has a tendency to reach particular equilibrium values given by the factors affecting extinction, colonization and (eventually) speciation rates, any change of these factors attributable to human activities necessarily affects resulting equilibrium species richness. Human appropriation of net primary productivity decreases the amount of resources available for natural communities, thus decreasing equilibrium species richness (Miko & Storch, 2015). Species richness carrying capacity may also decrease as a result of increasing extinction rates by increasing resource fluctuations and disturbances. In contrast, elevated colonization rates attributable to the breaking of geographical barriers can elevate species richness carrying capacity. Moreover, anthropogenic changes may elevate evolution and speciation rates owing to increasing species hybridization and adaptations to new environments, possibly elevating global species richness (Thomas, 2017). Whether such changes are expected to be transient or permanent, and whether future global diversity will increase or decrease in a long term, depends on the interactions of factors setting the carrying capacity for species richness of Earth's landmasses and oceans. Understanding future changes of biodiversity on Earth thus requires an understanding of equilibrium diversity dynamics.

8 | CONCLUSION

Macroecology deals with emergent general properties of aggregate ecological entities (McGill, 2019). Species richness is a prominent example of such an emergent property. Its large-scale variation is predictable and consistently linked to geographical environmental variation, namely climate, topography and resource availability. To explain such generalities, a similarly general principle is needed that goes beyond idiosyncrasies of individual taxa, regions and historical evolutionary pathways.

Here, we have argued that the concept of species richness carrying capacity represents such a general principle and can be used as a foundation for comprehensive macroecological theory on biodiversity dynamics. The equilibrium theory of biodiversity dynamics is a promising example of a macroecological theory relying on this concept. Species richness carrying capacity (i.e., stable diversity equilibrium) is an attractor of biodiversity dynamics, meaning that species richness has a tendency to approach it and fluctuate around it regardless of particular diversification pathways and initial historical settings. The diversity of individual taxa can vary tremendously across time and space, being affected by a multitude of climatic, topographic and historical factors in addition to biotic interactions. However, general properties of such dynamics and resulting macroecological patterns are governed by the existence of stable equilibria (i.e., species richness carrying capacity). These equilibria are determined by the balance of diversity-dependent processes of speciation, colonization and extinction modulated by environmental factors, the most important of which are temperature, topography, resource abundance and environmental stability. Such equilibria exist even if increasing the number of species increases the capacity of a given community to use the available resources. Diversity equilibria that emerge via the interplay of basic ecological and evolutionary processes provide an important baseline for predictive macroecological theory.

ACKNOWLEDGMENTS

This research was supported by the Czech Science Foundation (grant no. 16-26369S). The authors largely benefitted from the discussions within the Network of Ecological Theory Integration (NETI) group as well as within the sELDIG group supported by the sDiv (Leipzig, Germany).

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BIOSKETCH

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How to cite this article: Storch D, Okie JG. The carrying capacity for species richness. *Global Ecol Biogeogr.* 2019;28:1519–1532. https://doi.org/10.1111/geb.12987