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REVIEW AND SYNTHESIS

The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship

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Abstract

Species richness increases with energy availability, yet there is little consensus as to the exact processes driving this species–energy relationship. The most straightforward explanation is the more-individuals hypothesis (MIH). It states that higher energy availability promotes a higher total number of individuals in a community, which consequently increases species richness by allowing for a greater number of species with viable populations. Empirical support for the MIH is mixed, partially due to the lack of proper formalisation of the MIH and consequent confusion as to its exact predictions. Here, we review the evidence of the MIH and evaluate the reliability of various predictions that have been tested. There is only limited evidence that spatial variation in species richness is driven by variation in the total number of individuals. There are also problems with measures of energy availability, with scale-dependence, and with the direction of causality, as the total number of individuals may sometimes itself be driven by the number of species. However, even in such a case the total number of individuals may be involved in diversity regulation. We propose a formal theory that encompasses these processes, clarifying how the different factors affecting diversity dynamics can be disentangled.

Keywords

Abundance, biodiversity patterns, climate, diversity equilibria, environmental productivity, extinction, latitudinal diversity gradient, speciation, species–energy relationship.

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> *What then checks an indefinite increase in the number of species? The amount of life (I do not mean the number of specific forms) supported on an area must have a limit, depending so largely as it does on physical conditions; therefore, if an area be inhabited by very many species, each or nearly each species will be represented by few individuals; and such species will be liable to extermination from accidental fluctuations in the nature of the seasons or in the number of their enemies.*
>
> *Darwin 1859, Sixth edition*

INTRODUCTION

During the last few decades, enormous effort has been put into deciphering the most important environmental factors responsible for spatial variation in biodiversity. The general consensus is that climate-related variables have the strongest effect on geographic patterns in species richness (Currie 1991; Waide *et al.* 1999; Hawkins *et al.* 2003; Currie *et al.* 2004; Storch 2012). Since most of these variables are related to various energy measures, the number of species has been regarded as being controlled by the total energy available for a community (Currie 1991). The most straightforward idea linking energy availability and diversity is that energy availability is equivalent to the rate of flow of resources through an ecosystem, which limits the total number of individuals that a community can maintain within a region. Total number of individuals in turn limits the number of species that can have viable populations in that environment (Gaston 2000). In other words, a low total number of individuals cannot support a high number of species, because if there were a high number of species, some species would have such small populations that they would quickly go extinct (Box 1). This idea that spatial variation in species richness is mediated by environmentally dependent variation in the total number of individuals of communities due to the above mechanism has been termed 'the more-individuals hypothesis' (Srivastava & Lawton 1998) and has been regarded as a first-order explanation of diversity patterns (Gaston 2000).

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Box 1 Viable populations and the relationship between population size and extinction probability

The assumption that species with low population sizes have higher probability of extinction lies in the very core of many components of ecological theory including the theory of island biogeography (MacArthur & Wilson 1967), and comprises the background of explanations of many macroecological patterns (Brown 1995; Gaston & Blackburn 2000). Some authors attribute high extinction probability of small populations to genetic or behavioural effects, namely to accumulation of deleterious mutations or to the breakdown of social structure and/or inability of finding mating partners, respectively. The latter leads to the Allee effect, that is, the positive density dependence in population growth, so that the smaller the population, the more its size further decreases. However, the negative relationship between population size and extinction probability is more general and goes beyond these effects (which are characteristic for very small populations of a subset of taxa). It can to a large extent be interpreted as a statistical effect driven by demographic and environmental stochasticity, leading to population fluctuations which with higher probability lead to extinction for population sizes which are closer to zero. The term ‘viable population’ is thus rather relative, comprising always a particular time window and a probability that population of given size goes extinct within that window. All populations have non-zero probabilities of going extinct within the time window, but these probabilities decrease with their sizes. Theoretical development of the more-individuals hypothesis thus requires explicit dealing with extinction probabilities which goes beyond the simple notion of the number of viable populations.

Although the term ‘the more-individuals hypothesis’ (MIH) has been coined relatively recently (Srivastava & Lawton 1998), the idea itself has a long history, dating as far back as Darwin in the *Origin of Species* (see quote above). Hutchinson (1959) later argued that ‘if the fundamental productivity of an area is limited by a short growing season to such a degree that the total biomass is less than under more favourable conditions, then the rarer species in a community may be so rare that they do not exist’. Wright (1983) assumed that energy, expressed as ecosystem productivity, together with island area determine species’ population sizes and consequently extinction rates on islands, so that islands with higher total productivity will support more species with viable populations than islands with lower amounts of energy. The resulting species richness was therefore assumed to be affected by energy-dependent extinction rates, thereby providing the mechanism for the species–energy relationship. The species–energy relationship has sometimes been used as a synonym for the MIH (Currie *et al.* 2004). However, energy can affect species richness through several ways, not necessarily only through the total numbers of individuals (Allen *et al.* 2002; Evans *et al.* 2005a; Clarke & Gaston 2006; Storch 2012). By the species–energy relationship we thus hereafter mean the observed diversity pattern, that is, the positive correlation between various energy measures and species richness. The MIH is then the most straightforward explanation for this pattern but certainly not the only one.

Here we review tests of the MIH, quantify the support for various predictions purported to follow from the MIH and evaluate the reliability of these predictions. Furthermore, we reveal problems and commonly overlooked nuances related to the concept and its testing, showing that many of the proposed tests have been inappropriate, following from the lack of a proper formalisation of the MIH and varying and often contradictory formulations of the exact mechanism of the MIH. To overcome this problem, we propose a formal framework for the diversity dynamics mediated by the number of individuals, with the aim to clarify how the complex relationships between energy availability, community abundance and species richness can be disentangled and tested. Because population sizes and the total number of individuals in a community are fundamental variables in ecological theory (e.g. Harte *et al.* 2008; see Box 2), are commonly estimated in observational ecology, vary by many orders of magnitude across the globe and are changing in response to climate change, clarifying how patterns of abundance can shape patterns of biodiversity and their response to changing conditions should be a crucial research direction for ecology.

TESTING THE MORE-INDIVIDUALS HYPOTHESIS

We can distinguish two classes of studies aiming to test the MIH. The first class comprises small-scale, mostly experimental studies testing whether an increase in resource levels leads to an increase in the number of individuals of a community (hereafter *J*) and eventually an increase in the number of species *S*. The purpose of such studies is thus to establish whether theorised mechanisms of the MIH have the potential to generate species richness patterns. For instance, Srivastava & Lawton (1998) manipulated resource levels in dendrotelms to evaluate whether the abundance and species richness of aquatic invertebrates increase with increasing resource availability. Similarly, McGlynn *et al.* (2010) manipulated food resources for ants in Costa Rican rainforest to determine how ant abundance and diversity respond to varying resource levels. Such studies often conclude that both community abundances and species richness indeed increase with increasing resource levels (Fig. 1), demonstrating that the MIH can feasibly provide an explanation for the species–energy relationship.

This finding is not particularly surprising, however, given that all populations depend on resources and consequently the addition of resources tends to attract more individuals, including individuals from previously unobserved or absent species. The more crucial issue, one which these experimental studies do not address, is whether the *observed positive geographic relationship* between energy (or resource) availability and species richness is actually driven by the proposed effect – i.e. it is mediated by the total number of individuals *J*. This is the topic of the second class of MIH tests. These studies are based on analyses of observational data in order to determine

Box 2 The relationship between the equilibrium diversity theory and the Maximum Entropy Theory of Ecology (METE)

The theory presented here explicitly deals with the relationships between energy availability E, total number of individuals within the taxon in focus J and number of species S. These three variables also form the basis of the derivation of various macroecological measures using the Maximum Entropy Theory of Ecology (METE; Harte *et al.* 2008, 2009; Harte 2011). Maximum entropy approach in general provides the least biased estimates of statistical distributions of variables in focus assuming given set of constraints concerning particular state variables. METE specifically assumes that these state variables are E, J and S; it considers these three variables to be given *a priori* for a large region, and using maximum entropy machinery it derives various metrics and relationships within that region, including patterns of intraspecific aggregation of individuals, species-area relationships and species-abundance distributions (SAD)(Harte 2011). In contrast, the approach presented here aims at deriving equilibrium values of both S and J assuming a given E and particular processes of species origination and extinction, as well as a particular relationship between S and the ability of the community to utilise resources, that is, to maintain given J by utilising a particular fraction of E (note that $J_{\max}$, i.e. the maximum number of individuals of given taxon, is equal to E/B, where B is mean individual metabolic rate; there is thus a direct link between E and J, although it comprises only a limit of all energy being completely utilised by the taxa under consideration). Our equilibrium theory of diversity dynamics is thus complementary to METE: it explicitly models the effect of E on equilibrium values of J and S, while METE takes all these values as state variables for deriving other macroecological metrics within a given region (community). In turn, the METE predicts a particular SAD (namely the log-series distribution), which can be taken as an input for our equilibrium diversity theory. It is thus intriguing to think about combining both the theories – one dynamical and the other statistical – to enable predictions of a wider range of macroecological patterns across various spatial and temporal scales.

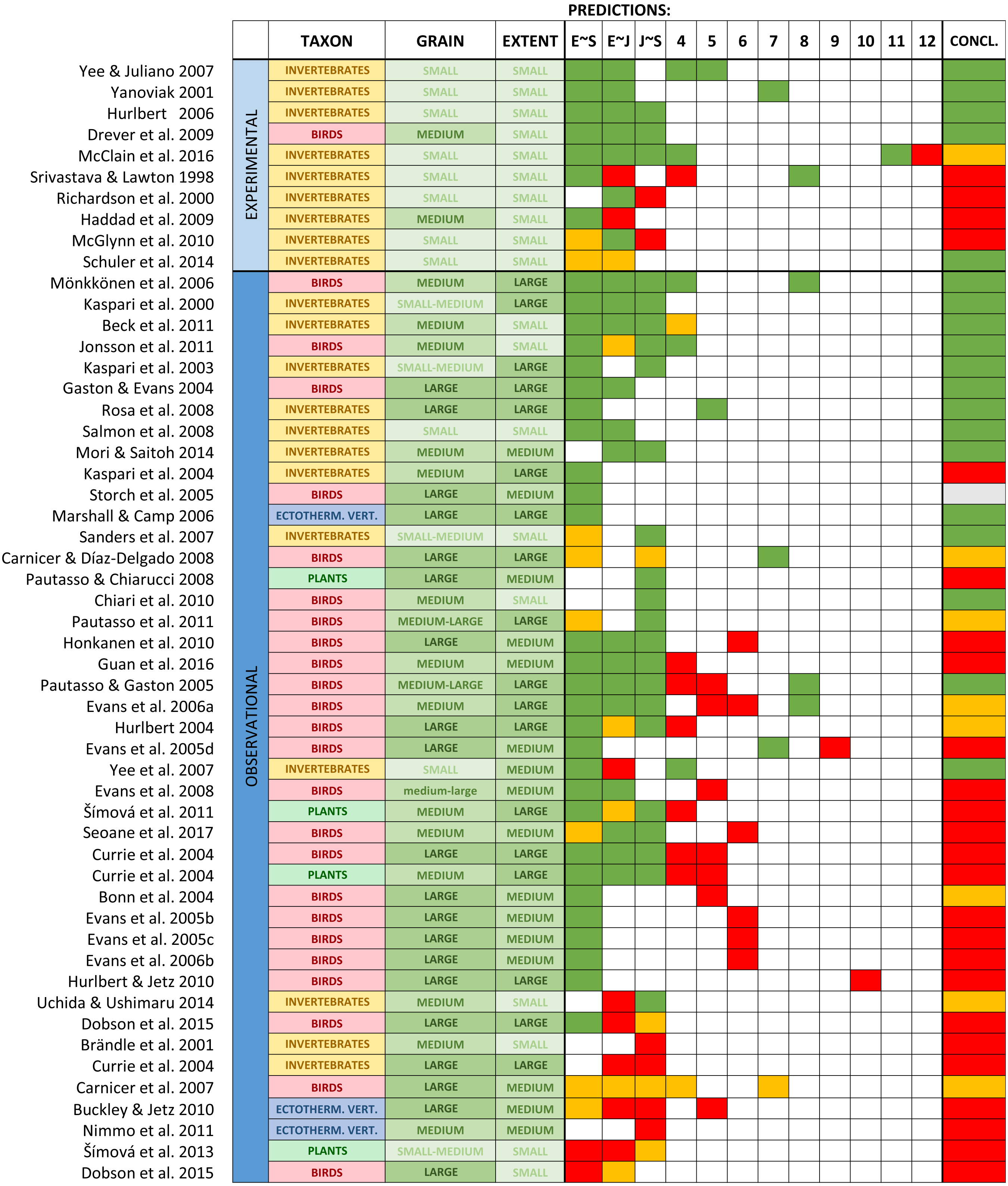
whether observed patterns conform to predictions assumed to follow from the MIH (Fig. 1). We next review the tests of these predictions; however, as we will show later, not all of these predictions actually follow from a rigorous formulation of the MIH.

Relationships between energy, community abundance and diversity

One prediction, tested in many studies, is that species richness S is positively related to energy availability or various surrogates of resource availability. Although the species–energy or species–productivity relationship is not always monotonically increasing and is quite variable, especially in plants (Adler *et al.* 2011; Šímová *et al.* 2013), a monotonically increasing species–energy relationship is observed quite regularly at broad spatial scales, at least on land. The situation can be more complicated in the ocean, where there may be contrasting patterns in nutrient availability and diversity (Angel 1993; Tittensor *et al.* 2010); nevertheless, more productive marine environments, such as coral reefs and estuaries, tend to have higher biodiversity than less productive environments, such as the open ocean and deep sea. In any case, since the positive correlation between energy availability and species richness is itself the pattern MIH is intended to explain, using this correlation to evaluate the MIH is a questionable approach. Robust tests of the MIH have to deal with all major component of the hypothesis, namely the patterns in the number of individuals (J), and how they are related to both energy availability (E) and species richness (S) (Currie *et al.* 2004).

Many studies found a positive relationship between availability of energy or resources and J. Total bird abundances increase with increasing normalised difference vegetation index (NDVI), a common surrogate of productivity (Hurlbert 2004; Evans *et al.* 2006a, 2008). Similarly, ant densities are positively related to net aboveground productivity (NAP) (Kaspari *et al.* 2000), and microbial community biomass and cell counts consistently increase with resource availability (Sinsabaugh *et al.* 2008; Serna-Chavez *et al.* 2013). On the other hand, the relationship between various energy surrogates and J is much weaker in many ectotherm animal taxa, like lizards (Buckley & Jetz 2010) and butterflies (Currie *et al.* 2004), and is often absent in plants (Šímová *et al.* 2013). A similar situation comprises the case of the relationship between J and S. Species richness generally correlates with total community abundance in birds (Evans *et al.* 2006a; Mönkkönen *et al.* 2006; Honkanen *et al.* 2010), ants (Kaspari *et al.* 2000, 2003) and river fish (Grenouillet *et al.* 2002), but the relationship is much weaker in butterflies (Currie *et al.* 2004), lizards (Buckley & Jetz 2010; Nimmo *et al.* 2011) and trees (Šímová *et al.* 2011) (Fig. 2). In microbes, some research suggested a positive relationship between S and J (Fierer & Lennon 2011; Locey & Lennon 2016), but Fuhrman *et al.* (2008) found a weak or non-existent relationship in marine plankton. The support for the MIH based on observed patterns of S and J thus seems to be mixed, differing between taxa and partly depending on the used measure of resource or energy availability (Fig. 3a,b).

The MIH assumes that energy availability E determines J, which is the key factor generating species richness patterns. It is thus expected that there should be a strong relationship between E and J, and also a tight relationship between J and S. In contrast, the relationship between E and S is predicted to be weaker, as this relationship is only indirect, mediated by J (Currie *et al.* 2004). However, in most cases we observe exactly the opposite, species richness being relatively tightly linked to the surrogates of energy availability, while J seems to be quite weakly related to energy availability and not very strongly correlated to species richness (Currie *et al.* 2004; Šímová *et al.* 2011; Storch 2012). Additionally, energy availability often has a significant effect on species richness even after accounting for statistical effects of J using a multiple regression (Pautasso & Gaston 2005;



					PREDICTIONS:												
		TAXON	GRAIN	EXTENT	E~S	E~J	J~S	4	5	6	7	8	9	10	11	12	CONCL.
Yee & Juliano 2007	EXPERIMENTAL	INVERTEBRATES	SMALL	SMALL	🟩	🟩		🟩	🟩								🟩
Yanoviak 2001		INVERTEBRATES	SMALL	SMALL	🟩	🟩					🟩						🟩
Hurlbert 2006		INVERTEBRATES	SMALL	SMALL	🟩	🟩	🟩										🟩
Drever et al. 2009		BIRDS	MEDIUM	SMALL	🟩	🟩	🟩										🟩
McClain et al. 2016		INVERTEBRATES	SMALL	SMALL	🟩	🟩	🟩	🟩							🟩	🟥	🟧
Srivastava & Lawton 1998		INVERTEBRATES	SMALL	SMALL	🟩	🟥		🟥				🟩					🟥
Richardson et al. 2000		INVERTEBRATES	SMALL	SMALL		🟩	🟥										🟥
Haddad et al. 2009		INVERTEBRATES	MEDIUM	SMALL	🟩	🟥											🟥
McGlynn et al. 2010		INVERTEBRATES	SMALL	SMALL	🟧	🟩	🟥										🟥
Schuler et al. 2014		INVERTEBRATES	SMALL	SMALL	🟧	🟧											🟩
Mönkkönen et al. 2006	OBSERVATIONAL	BIRDS	MEDIUM	LARGE	🟩	🟩	🟩	🟩				🟩					🟩
Kaspari et al. 2000		INVERTEBRATES	SMALL-MEDIUM	LARGE	🟩	🟩	🟩										🟩
Beck et al. 2011		INVERTEBRATES	MEDIUM	SMALL	🟩	🟩	🟩	🟧									🟩
Jonsson et al. 2011		BIRDS	MEDIUM	SMALL	🟩	🟧	🟩	🟩									🟩
Kaspari et al. 2003		INVERTEBRATES	SMALL-MEDIUM	LARGE	🟩		🟩										🟩
Gaston & Evans 2004		BIRDS	LARGE	LARGE	🟩	🟩											🟩
Rosa et al. 2008		INVERTEBRATES	LARGE	LARGE	🟩				🟩								🟩
Salmon et al. 2008		INVERTEBRATES	SMALL	SMALL	🟩	🟩											🟩
Mori & Saitoh 2014		INVERTEBRATES	MEDIUM	MEDIUM		🟩	🟩										🟩
Kaspari et al. 2004		INVERTEBRATES	MEDIUM	LARGE	🟩												🟥
Storch et al. 2005		BIRDS	LARGE	MEDIUM	🟩												⬜
Marshall & Camp 2006		ECTOTHERM. VERT.	LARGE	LARGE	🟩												🟩
Sanders et al. 2007		INVERTEBRATES	SMALL-MEDIUM	SMALL	🟧		🟩										🟩
Carnicer & Díaz-Delgado 2008		BIRDS	LARGE	LARGE	🟧		🟧				🟩						🟧
Pautasso & Chiarucci 2008		PLANTS	LARGE	MEDIUM			🟩										🟥
Chiari et al. 2010		BIRDS	MEDIUM	SMALL			🟩										🟩
Pautasso et al. 2011		BIRDS	MEDIUM-LARGE	LARGE	🟧		🟩										🟧
Honkanen et al. 2010		BIRDS	LARGE	MEDIUM	🟩	🟩	🟩			🟥							🟥
Guan et al. 2016		BIRDS	MEDIUM	MEDIUM	🟩	🟩	🟩	🟥									🟥
Pautasso & Gaston 2005		BIRDS	MEDIUM-LARGE	LARGE	🟩	🟩	🟩	🟥	🟥			🟩					🟩
Evans et al. 2006a		BIRDS	MEDIUM	LARGE	🟩	🟩	🟩		🟥	🟥		🟩					🟧
Hurlbert 2004		BIRDS	LARGE	LARGE	🟩	🟧	🟩	🟥									🟧
Evans et al. 2005d		BIRDS	LARGE	MEDIUM	🟩						🟩		🟥				🟥
Yee et al. 2007		INVERTEBRATES	SMALL	MEDIUM	🟩	🟥		🟩									🟩
Evans et al. 2008		BIRDS	medium-large	MEDIUM	🟩	🟩			🟥								🟥
Šímová et al. 2011		PLANTS	MEDIUM	LARGE	🟩	🟧	🟩	🟥									🟥
Seoane et al. 2017		BIRDS	MEDIUM	MEDIUM	🟧	🟩	🟩			🟥							🟥
Currie et al. 2004		BIRDS	LARGE	LARGE	🟩	🟩	🟩	🟥	🟥								🟥
Currie et al. 2004		PLANTS	MEDIUM	LARGE	🟩	🟩	🟩	🟥	🟥								🟥
Bonn et al. 2004		BIRDS	LARGE	MEDIUM	🟩				🟥								🟧
Evans et al. 2005b		BIRDS	LARGE	MEDIUM	🟩					🟥							🟥
Evans et al. 2005c		BIRDS	LARGE	MEDIUM	🟩					🟥							🟥
Evans et al. 2006b		BIRDS	LARGE	MEDIUM	🟩					🟥							🟥
Hurlbert & Jetz 2010		BIRDS	LARGE	LARGE	🟩									🟥			🟥
Uchida & Ushimaru 2014		INVERTEBRATES	MEDIUM	SMALL		🟥	🟩										🟧
Dobson et al. 2015		BIRDS	LARGE	LARGE	🟩	🟥	🟧										🟥
Brändle et al. 2001		INVERTEBRATES	MEDIUM	SMALL			🟥										🟥
Currie et al. 2004		INVERTEBRATES	LARGE	LARGE		🟥	🟥										🟥
Carnicer et al. 2007		BIRDS	LARGE	MEDIUM	🟧	🟧	🟧	🟧			🟧						🟧
Buckley & Jetz 2010		ECTOTHERM. VERT.	LARGE	MEDIUM	🟧	🟥	🟥		🟥								🟥
Nimmo et al. 2011		ECTOTHERM. VERT.	MEDIUM	MEDIUM			🟥										🟥
Šímová et al. 2013		PLANTS	SMALL-MEDIUM	SMALL	🟥	🟥	🟧										🟥
Dobson et al. 2015		BIRDS	LARGE	SMALL	🟥	🟧											🟥

Figure 1 The reviewed studies sorted (within the blocks of experimental and observational studies) from most supportive to least supportive, according to the ratio of the number of predictions met to the number of predictions not met. GRAIN refers to the unit of analysis; small: 0–1 m, medium: 1 m–10 km, large: from 10 km. EXTENT refers to the total area explored; small: local to landscape (0–50 km), medium: regional (50–2000 km), large: continental to global (more than 2000 km). PREDICTIONS refers to individual predictions tested, so that the colour refers to the result; green: the prediction was met, orange: the prediction was met only for some grain/taxon (or the relationship was weak), red: the prediction was not met. Predictions 4–12 correspond to the numbered predictions in Fig. 3c. CONCLUSION refers to the interpretation of the results by the authors (green = MIH supported, orange = MIH partly supported, red = results are not consistent with the MIH).

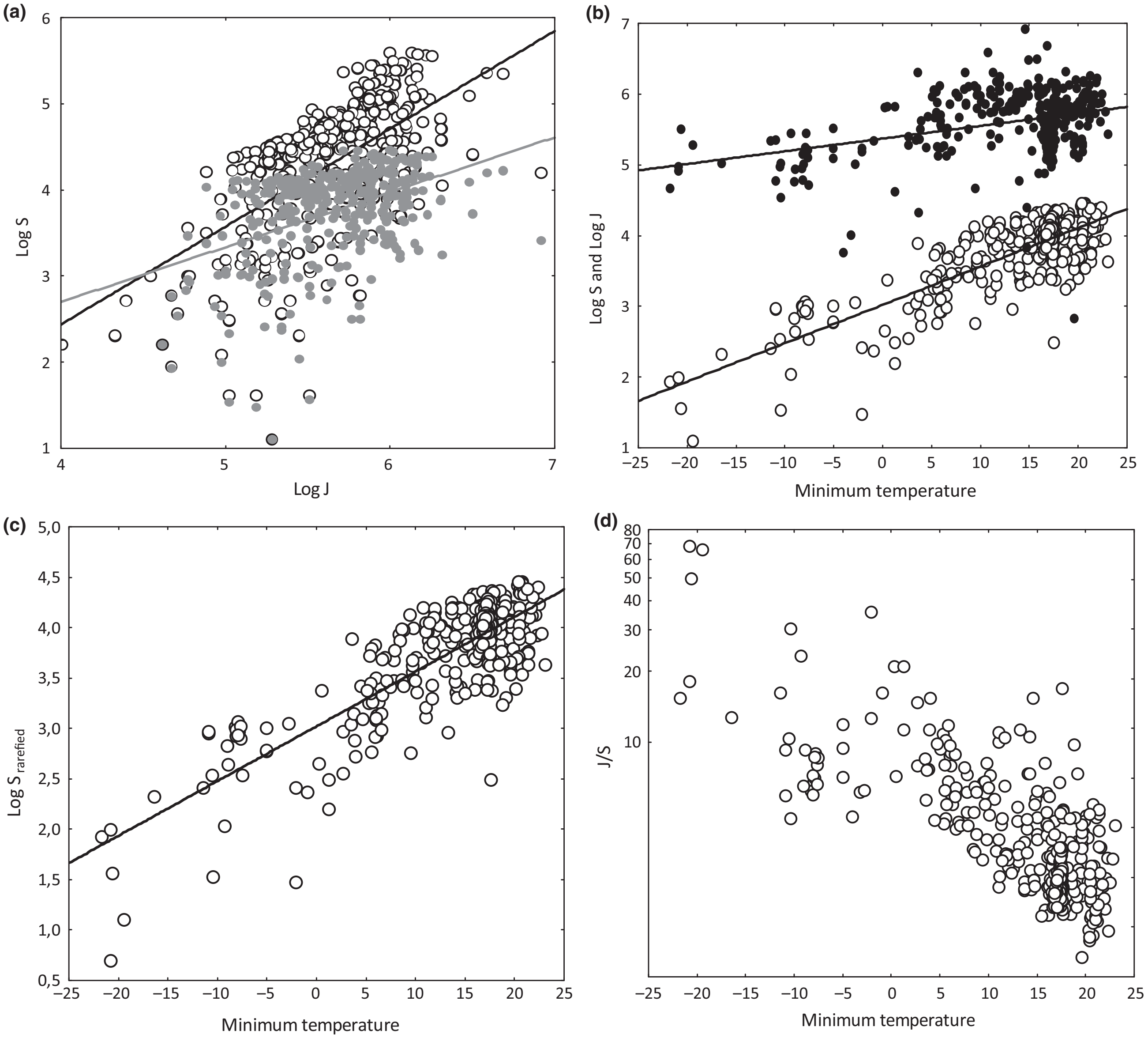


Figure 2 An example of observed relationships between S, J and environmental conditions from forest plots worldwide. (a) The relationship between J and S on a log–log scale. The slope of the log$S$–log$J$ relationship for rough species richness data (white circles and black line) is 1.14, indicating a supralinear relationship in which species richness increases faster than the number of individuals. Notably, the relationship between J and S is positive even in the case of rarefied species richness data (grey dots and grey line) where the number of individuals was controlled for by calculating mean species richness per 100 individuals (Šímová *et al.* 2011) (although the slope 0.64 indicates a sublinear relationship in this case). (b) These patterns can be explained by the fact that while both S (white circles) and J (black dots) increase with minimum temperature, the relationship is much weaker in the case of J. This leads to a positive relationship between minimum temperature and rarefied species richness (c) as well as to a negative relationship between minimum temperature and mean population size J/S (d). Minimum temperature is shown here because it was the single best environmental predictor of both variables and represents a good surrogate of energy availability in the environment (forests) without a strong water limitation. Data are from Gentry plots, which are 0.1 ha in size (see Šímová *et al.* 2011 for data and analysis details).

Šímová *et al.* 2011) or rarefaction (Hurlbert 2004; Šímová *et al.* 2011) (Fig. 2). These findings have been put forth as the strongest argument against the validity of the MIH (Currie *et al.* 2004), as they seem to indicate that species richness patterns are not mediated by J.

Testing other MIH predictions

Besides the abovementioned relationships between E, J and S, some other predictions presumed to stem from the MIH have been tested (Fig. 3c). Some authors tested the slopes of the relationship between J and S and compared them with the slopes derived from various theoretical assumptions. However, various theories differ as to the predicted relationship between J and S. One possibility (Srivastava & Lawton 1998) is that S should be proportional to the logarithm of J, according to the derivation of log-series species-abundance distribution (SAD) by Fisher *et al.* (1943). In contrast, Currie *et al.* (2004) assumed a power-law relationship with a slope of about one-quarter based on a

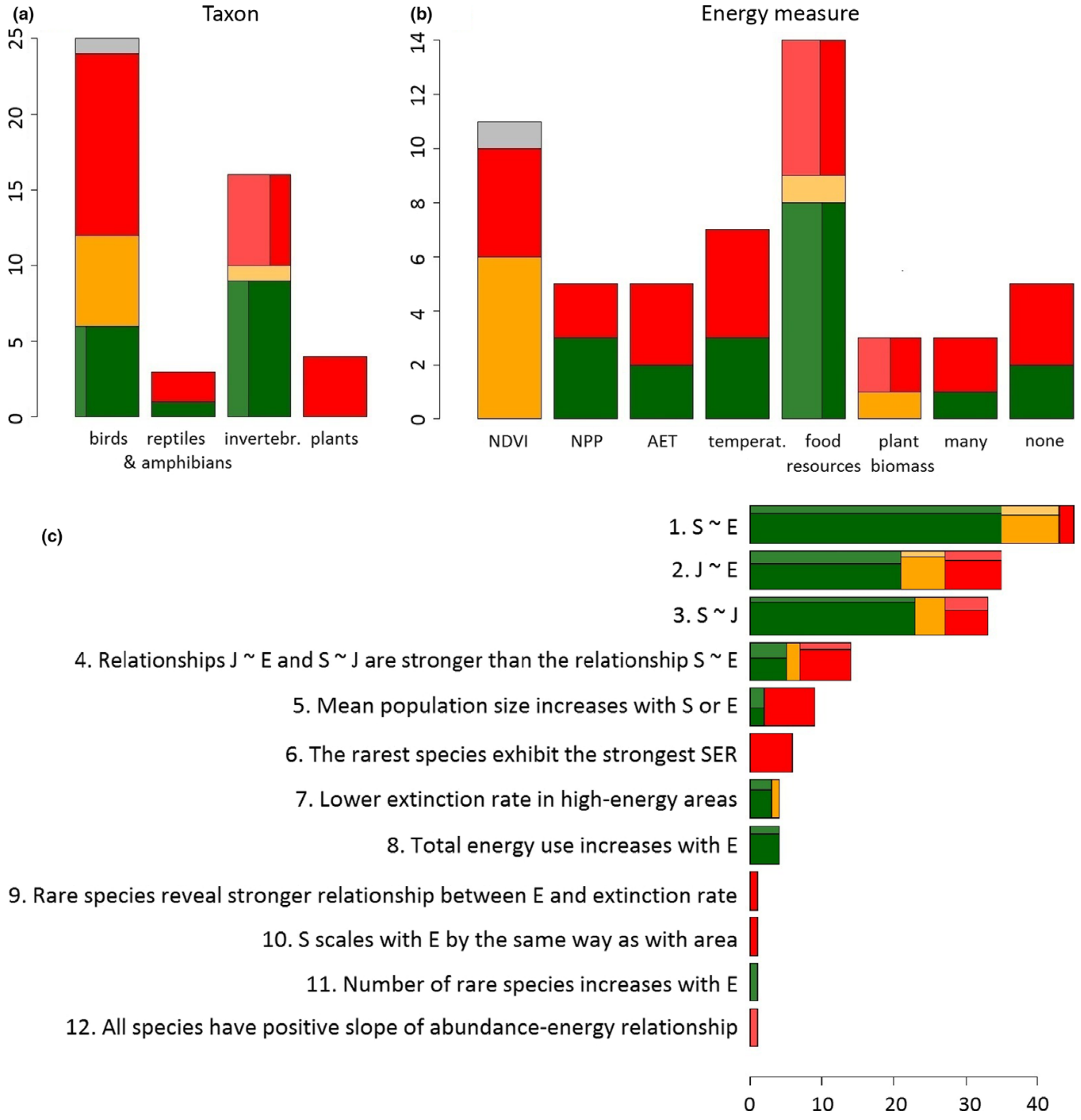


Figure 3 Top: Overview of the studies testing the MIH, grouped by the measure used to estimate energy availability (a) and taxa (b), and the reported conclusion provided by the authors concerning the validity of the MIH (green = consistent with the MIH; orange = partly consistent; red = inconsistent with the MIH; grey = could not be evaluated; the lighter hue on the left side of respective bars refers to respective proportion of experimental studies). Support for the MIH has been reported in less than half of all studies, relatively independently of taxon and the measure used. Bottom (c): Results of individual predictions that the authors of the studies considered as following from the MIH (green: the prediction was met; orange: the prediction was met only for some grain/taxon or the relationship was weak; red: the prediction was not met; the lighter hue on the upper part of respective bars refers to respective proportion of experimental studies). Note that not all the predictions follow from a proper formalisation of the MIH (see the text): while the rejection of first four predictions indicates that species richness variation is not driven by variation in available energy E and total number of individuals J (and thus these predictions can evaluate the strict formulation of the MIH), remaining predictions do not follow from a proper formalisation of the MIH and their rejection does not invalidate the MIH. Neither prediction can evaluate the role of J for species richness regulation, and the positive test (the fact that a prediction holds) does not mean that the number of individuals is the actual driving variable.

derivation of the lognormal SAD (Preston 1962). Although Currie *et al.* (2004) claim that the observed slopes are considerably higher (in accord with their statement that J is, in contrast to S, largely independent of energy availability), some studies are more or less in accord with this slope (Hurlbert 2004; Pautasso *et al.* 2011).

Some authors have argued that since mechanisms of the MIH reflect abundance-dependent extinction rates, relationships between *S*, *J* and *E* should differ between rare and common species. Evans *et al.* (2005b) argued that *S* should be more tightly linked to *E* in rare species, as their presumed higher probability of extinction resulting from their low abundances should increase the likelihood that they have had the chance to experience the abundance-related extinction. The logic of this reasoning is not entirely clear and in fact an opposite pattern has been observed (Evans *et al.* 2005b,c, 2006a,b; Honkanen *et al.* 2010; Seoane *et al.* 2017). Evans *et al.* (2005d) also argued that extinction rates should be higher in less productive environment and reported this pattern for British birds. The problem of all of these predictions is that it is difficult to evaluate if they truly represent a necessary component of the MIH before a particular theory concerning diversity dynamics is formulated.

Some formulations of the MIH argue that higher *E* should lead to higher population abundances or densities of individual species, leading to lower species extinction rates (e.g. Evans *et al.* 2005b,c,d). The abovementioned observation that the total number of individuals *J* often does not covary too strongly with *E* or *S* implies that mean population sizes of individual species actually mostly do not increase with energy availability (otherwise *J* would increase with *E* even more steeply than *S*). Indeed, mean population size of species seems to be invariant with respect to energy availability in birds (Pautasso & Gaston 2005; Evans *et al.* 2006a, 2008), and a negative relationship between productivity and mean population sizes is common in plants as well as other ectotherm taxa (Currie & Fritz 1993; Allen *et al.* 2002). Individual population sizes also seem to decrease towards the tropics (Currie *et al.* 2004), which contradicts the idea that the MIH is a major effect driving the latitudinal diversity gradient. These observations indicate at least that the processes generating species richness patterns are more complex and do not comprise only the population size-dependent extinction rates; otherwise high species richness (e.g. in the tropics) would not be associated with generally smaller populations, which are more prone to extinction. The role of *J* as well as individual population sizes in these processes is yet unclear.

PROBLEMS WITH MIH TESTING

Although the results of the tests of the MIH reviewed above are mixed (Fig. 3c), the overall conclusion is that the MIH does not seem to be a general explanation of species richness patterns – even though *S* is often positively related to *E* and *J*, diversity patterns do not seem to be mediated by *J*. However, authors differed in the exact predictions they assumed to stem from the MIH, and even in the exact meaning of the MIH. There are thus several issues that must be considered before the whole concept can be rejected and before we start to understand the role of abundance in biodiversity patterns.

Problem I: Appropriate spatial scales and energy measures

The MIH assumes extinction dynamics mediated by population sizes. However, it is not clear at what spatial scales these processes operate. Population densities within small sampling units may not be particularly relevant for the extinction dynamics, as extinction probabilities depend also on the number of individuals in surrounding areas, which can decrease local extinction probabilities via the rescue effect (Brown & Kodric-Brown 1977). Thus, biodiversity dynamics necessarily reflect both small and large spatial scales, with species geographic range sizes, metapopulation connectivity, and local densities interactively influencing species extinctions. The productivity-diversity relationship is scale-dependent (Chase & Leibold 2002), often being hump-shaped at smaller scales, but monotonically increasing and generally stronger at larger scales (Rahbek & Graves 2000; Mittelbach *et al.* 2001; Belmaker & Jetz 2011). It is thus reasonable to assume that the MIH can operate mostly at these scales (Box 3).

Complications lie also in the very concept of energy availability. The energy effectively available to a community obviously varies by the taxa and trophic level of communities. Thus, although *E* can be sometimes proportional to net primary productivity (NPP) of a given ecosystem, different taxa utilise different portions of available resources. Moreover, the MIH implicitly assumes that available energy is shared among community members, thus affecting their population sizes via interspecific competition. This may be a reasonable assumption for a particular trophic level, but it is more problematic for multitrophic communities where higher abundance at one level may actually increase energy availability for higher levels. In the strict sense, the MIH should therefore comprise only communities on a particular trophic level, although many authors tested it using multitrophic communities (e.g. Hurlbert 2004; Evans *et al.* 2005b,c,d, 2008).

Some authors have assumed that an essential condition of the MIH is a proportionality between the total energy potentially available to communities (i.e. NPP or ecosystem-level productivity of the trophic level the communities feed on) and the energy actually utilised by communities, which is more directly related to *J* (e.g. Srivastava & Lawton 1998); however, as long as *J* varies with energy availability, a condition of proportionality is not necessary. Additionally, although NPP may represent a good approximation of the energy which is available for consumers (and generally for all higher trophic levels, assuming energy is proportionally transferred to higher trophic levels), it is not clear what represents energy availability for autotrophs, that is, organisms which themselves generate NPP (Šímová & Storch 2017). Moreover, NPP is notoriously difficult to accurately measure or estimate, and various productivity estimates considerably vary in their reliability (Šímová & Storch 2017).

Problem II: What are the exact quantitative predictions?

One of the main reasons why the MIH could not be conclusively evaluated is that it has not been properly formalised and various authors differed as to its exact formulation. Almost every study has formulated the MIH slightly differently. Some authors consider the MIH as a pure sampling effect (see Hutchinson's quote above): if a community is assembled by sampling individuals from a source pool, then a sample with low number of individuals

Box 3 The MIH and spatial scale

Species richness patterns are scale-dependent (Rosenzweig 1995) and multiple pieces of evidence suggest that the relationship between the number of individuals and species richness also varies with spatial scale. There are three interrelated reasons to expect that the diversity dynamics assumed by the MIH are reasonable mostly at large spatial scales:

(1) Species richness correlates with energy-related climatic variables much better at large spatial scales than small scales (e.g. Field *et al.* 2009; Belmaker & Jetz 2011; Jetz & Fine 2012). Moreover, when comparing large and independent biogeographic units differing in area, the combination of area and primary productivity provides a very strong statistical predictor of diversity (Wright 1983; Rosenzweig *et al.* 2012).

(2) If we assume that species richness patterns are mediated by total number of individuals, species richness should be related to area similarly as to energy availability, since total number of individuals is proportional to area. However, slopes of the species-area relationship (SAR) are high and comparable with slopes of the species–productivity relationship only for large or isolated areas (Rosenzweig 1995; Storch *et al.* 2012). In contrast, SAR slopes are much lower at small scales within individual biogeographic regions, and area is not interchangeable with productivity at these scales (Storch *et al.* 2005; Hurlbert & Jetz 2010; Storch 2016), probably as a result of homogenising effects of migration.

(3) The MIH explicitly deals with the concept of viable populations and species extinctions (Box 1) and these concepts are relevant mostly when whole species populations are considered, and they do not work very well at local scales where population persistence is dependent on immigration from neighbouring communities.

The MIH thus seems more relevant for patterns of regional species richness driven mostly by evolutionary processes of speciation and regional extinction (Rosenzweig 1995), rather than to patterns of local richness generated by processes of immigration and local extinction. It is not easy to distinguish these levels in practice, as there is a natural continuum across spatial scales (reflected by the SAR). However, large land units like continents, remote islands or biogeographic regions represent natural evolutionary arenas for the emergence of regional species richness patterns driven by large-scale diversity dynamics (Rosenzweig 1995). There is also evidence that biomes are sufficiently separated to be treated as such units, as most species are confined to separate biomes and evolutionary transitions from one biome to another are rare (Crisp *et al.* 2009).

These considerations do not necessarily imply that number of individuals does not play some role for species richness patterns at smaller spatial scales, but the simple and straightforward effects assumed by the MIH are probably masked by the complexities of metacommunity dynamics characterised by pertinent migration between local communities (see Supplementary Information). For local scales, it can thus be necessary to model both the regional diversity dynamics, which set the upper limit to local diversity, and the processes that determine diversity patterns concerning the subset of species co-occurring locally (Harte *et al.* 2008; Storch *et al.* 2008; McGill 2010).

will probably not contain the rarest species from the source pool, and thus will have consequently lower S than a large sample. In contrast, other authors assume that more complex evolutionary and ecological processes including extinction dynamics play a role (these two versions of the MIH may actually refer to different spatial scales; see Box 3). Even among these papers, there are important differences in the argued concepts, particularly in terms of the role of individual population sizes. As mentioned above, the most general formulation of the MIH proposes that higher energy availability supports communities with greater total numbers of individuals, which consequently allows communities to be divided into higher numbers of species with populations that are still viable (e.g. Gaston 2000; Gaston & Evans 2004; Hurlbert 2004; Šímová *et al.* 2011) (Box 1). However, this formulation does not imply that higher energy availability necessarily leads to *higher abundances of individual species* (which, according to the abovementioned authors, should lead to lower extinction rates and consequently higher species richness). In fact, as we will show below, equilibrium population sizes, and consequently mean species extinction probabilities, can be on average the same in low-energy and high-energy environment, even if both J and S differ.

Different formulations of the MIH result in different predictions. It is relatively straightforward to make predictions when the formulation centres around a sampling effect, since a sampling effect is relatively easy to simulate or quantify analytically. Still, making quantitative predictions of the precise relationship between S and J requires assuming a particular form of the species-abundance distribution (SAD), which is a controversial and non-trivial matter (McGill *et al.* 2007; Šizling *et al.* 2009). Moreover, sampling effects may be relevant at local spatial scales, but the SAD is itself a result of the processes of speciation or colonisation, extinction and community assembly, so that the sampling from an *a priori* given SAD does not represent a complete explanation of the observed species richness patterns at larger scales. A more compelling quantitative formulation of the MIH is thus one based on quantitative theory that explicitly addresses the fundamental processes of speciation, colonisation and extinction, and the way they are modulated by the total number of individuals.

An example of a theory incorporating these processes and able to make predictions concerning how species richness depends on J (and also speciation rates and dispersal limitations) is neutral theory (Hubbell 2001). It predicts that S is a function of the product of J and per capita speciation rate v, and produces predictions concerning the SAD and spatial patterns in species distributions. However, neutral theory assumes equivalency of all individuals regardless of species identity (and thus also an equal access to all resources), and it is not clear what to expect if these assumptions are released. Even more importantly, neutral theory does not address potentially complex linkages between E and J, as J is given *a priori* within the model. Thus, more general and fundamental theory of diversity dynamics must be formulated before the MIH can be properly tested quantitatively.

Problem III: Directions of causality

The MIH, regardless of its exact formulation, assumes that the energy availability or environmental productivity affects the total number of individuals of a taxon. However, the biological mechanisms mediating the relationship between E and J across space and time are certainly more complex. Since each species has its own (meta)population dynamics, affected by other species and many other factors, variation in J reflects the aggregate of all these species-level dynamics – in other words, J is an emergent property of the dynamics rather than a driving variable. So, although J cannot be sustained in the long run beyond the limits given by the total rate of flux of available energy and individual energy consumption, J does not simply follow from ecosystem-level energy availability – it also depends on factors such as the appearance of new species with novel niches and the stochastic population dynamics of individual species. Since population sizes of individual species can considerably vary in time, sometimes even temporarily exceeding population carrying capacities, J can also vary considerably especially at smaller spatial scales. It is thus not surprising that variation in J has been observed to be partially decoupled from variation in S and E. However, species richness can be still affected by population size-dependent extinction dynamics driven by available resources, even if J temporarily varies.

More generally, a major challenge with formalising and evaluating the MIH has been how to address the intertwined causality between the primary variables under consideration. Most approaches have assumed that J is given *a priori* by energy availability in an ecosystem, and species richness then follows either from simple sampling or more complex dynamics involving population size-dependent extinction (Evans *et al.* 2005a). However, since J itself can be partially driven by these dynamics, the observed positive relationship between J and S can reflect the positive effect of S on J, as well or instead of effects of J on S (Šímová *et al.* 2011; Storch 2012) (Fig. 4). For instance, if there is a higher number of species in a community (for a reason unrelated to the total number of individuals J), then there is a higher chance that some species will utilise resources which would not be otherwise utilised, thereby elevating J, such as when a newly arriving bird species can utilise a food resource impossible for other birds to acquire (e.g. insects under the tree bark) or a plant that utilises nutrients which are unavailable for the other plants (e.g. nitrogen-fixing legumes). Another example consists of the potential effects of facilitative species interactions on resource utilisation. The fact that J can itself be dependent on the set of species within a given community means that there is a need to develop a more universal and comprehensive theoretical framework for diversity dynamics. Here, we sketch a conceptual outline for such a framework, aiming to enable the evaluation of which exact predictions follow from the effect of energy-related extinction dynamics assumed by the MIH.

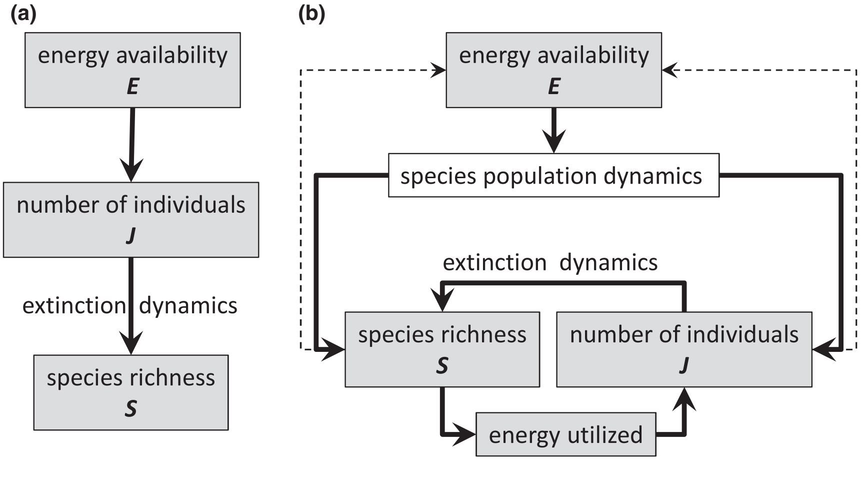


Figure 4 Classical view on the MIH (a) assumes that energy availability directly determines the total number of individuals J, and J then determines the number of species via extinction dynamics, so that lower numbers of individuals prohibit the persistence of many species with viable populations. In such a case, tight relationships between E and J and between J and S are expected, whereas the relationship between E and S is predicted to be weaker, as it is only indirect, mediated by J. The more realistic view (b), however, is that energy availability affects in complex ways species population dynamics, and both the number of individuals and number of species follow from these dynamics. Still, maximum number of individuals is limited by available energy, and the number of species is limited by the number of viable populations limited by J. However, S can in turn affect J, as higher numbers of species can utilise wider spectra of resources. In this scenario, the strength of relationships between E, J and S can vary depending on the importance of these causal links. Moreover, the exact relationship between these variables may be even more complex when considering multitrophic communities. For instance, consumer diversification may encourage producer diversification – and if higher producer diversity augments primary productivity, energy availability for consumers increases (left dashed arrow). Also, high J at one trophic level may affect energy availability at different trophic levels via trophic cascades (right dashed arrow).

A THEORETICAL FRAMEWORK FOR DIVERSITY DYNAMICS

General approach

Since the MIH explicitly assumes that species richness is limited by energy-driven total number of individuals, it represents an equilibrial view of diversity dynamics. Such a perspective does not assume that species richness is at equilibrium in all areas all of the time; rather, it assumes that species richness of communities hover around equilibria determined by the balance of the processes that add and remove species from the community, that is, speciation, colonisation and extinction. The existence and prevalence of diversity equilibria is debated (see Cornell 2013; Rabosky 2013; Harmon & Harrison 2015; Rabosky & Hurlbert 2015), but there is evidence to expect that such equilibria exist at least at large scales (Rosenzweig 1995; Rabosky & Hurlbert 2015). Such evidence stems from paleontological time-series (Alroy 2008), observed diversification slowdowns in species-level phylogenetic trees (McPeek 2008; Morlon *et al.* 2010; Machac *et al.* 2013, 2018) and from the apparent independence of many mutually consistent diversity patterns from particular histories of diversification (Hawkins *et al.* 2012; Belmaker & Jetz 2015; Oliveira *et al.* 2016).

Several models of equilibrium diversity dynamics have previously been proposed (Maurer 1989; Hubbell 2001; Nee 2006; Quental & Marshall 2010; Etienne *et al.* 2012; Cornell 2013; Rabosky 2013). All of them share several key features. First, the equilibrium follows from a negative diversity dependence stemming from the fact that for a given amount (or inflow) of resources, an elevated number of species necessarily leads to lower amounts of resources available for each species, leading to lower mean population sizes and consequently higher extinction probabilities (Fig. 5, see Darwin's quote above). Second, the equilibrium is dynamical, reflecting the balance between the input of species into the community (speciation and/or colonisation) and species loss, that is, extinction. Species richness then centres around the stable equilibrium value, since a further increase in S would lead to an increase in extinction rate (due to smaller average population sizes) above the instantaneous rates of colonisation and speciation.

Perhaps the most comprehensive theory of biodiversity dynamics is the neutral theory (Hubbell 2001), which is an example of individual-based models and has the advantage of being able to predict also abundance patterns. However, neutral theory is quite specific in its assumptions (see above),

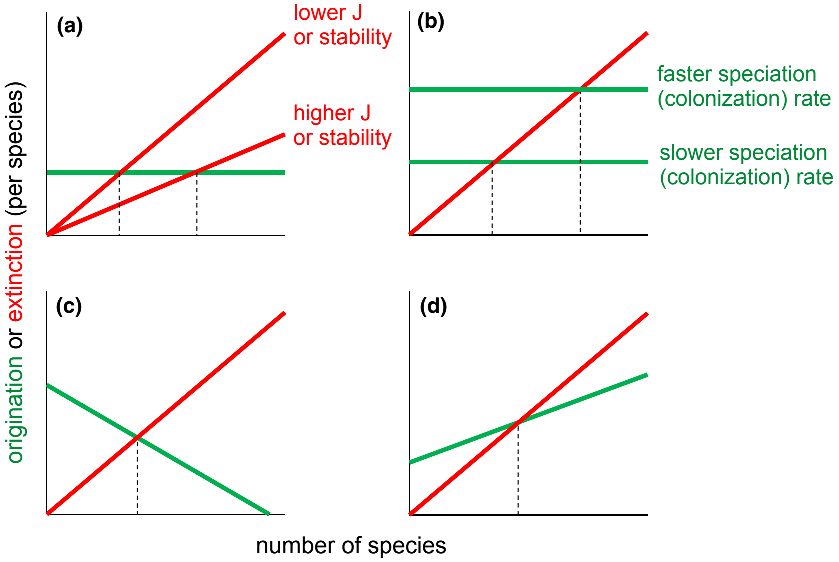


Figure 5 Illustration of the concept of equilibrium diversity dynamics, implicit in most models. For a given total amount of resources and given J, per-species extinction rates (red lines) increase with species richness (they are diversity-dependent), because mean population size N ($=J/S$) necessarily decreases with S. All the models of diversity dependence thus implicitly assume interspecific competition that affects population sizes due to the limited total amount of resources. Equilibrium diversity is attained where extinction rate is balanced by rate of speciation or immigration (or, generally, the origination rate, green), so that any increase in S above the equilibrium value leads to the increase in extinction rate above the level of origination rate (it is thus a stable equilibrium). (a) Variation of equilibrium diversity can be due to varying extinction rates, for example, due to varying environmental stochasticity, or due to different total number of individuals, as assumed by the MIH. The diversity-dependent per-species extinction rate then increases with S more steeply under lower resource levels (and thus low J) or more variable environment, because in these cases, the populations are smaller (mean population size J/S is lower) for given S or are more prone to environmental fluctuations, respectively. (b) Equilibrium diversity can be driven also by varying speciation or immigration rates, which may not itself depend on species richness. (c) However, the origination rate can be a decreasing function of species richness, for example, in the case of speciation being more probable in large populations in which more mutations occur. Such a relationship is expected also at small spatial scales where colonisation predominates, and equilibrium dynamics essentially follows the theory of island biogeography (then the decrease results from a decreasing number of species from the source pool that are not already present in the community; MacArthur & Wilson 1967). It is thus reasonable to assume that the exact shape of the origination function will be scale-dependent. (d) The origination function can potentially also increase with S (and thus with decreasing mean N), for example, due to higher probability of speciation in small populations or due to the situation when 'diversity begets diversity' (Calcagno *et al.* 2017; Schemske *et al.* 2009). Still, the stable equilibrium is attained when the intercept is higher and the slope is lower in the origination function than in the extinction function.

unable to encompass the situations when species differ in their habitat and resource requirements (niches), and it does not address all the potentially important and non-trivial links between E, J and S. We thus propose a species-based theoretical framework that circumvents these issues by making only broad assumptions concerning key ecological processes, without being specific about the underlying mechanisms. Our framework could thus be considered in a sense a universal theory or meta-theory, since the equilibrium diversity dynamics in other diversity theories and models including species-based simulations (e.g. Hurlbert & Stegen 2014a,b) are encompassed by our theory. Our aim is not to replace these particular models but to provide a more general coarse-grained framework that encompasses a broader range of processes without losing the ability to make predictions, in order to help to disentangle the role of number of individuals and energy availability from other major processes in regulating diversity patterns.

The theory

Our theoretical framework deals with the processes affecting the number of species in a given community, that is, speciation, colonisation and extinction. Since the MIH is more relevant at large spatial scales (Box 3), we focus our presentation on such scales and ignore the effect of colonisation, assuming that large-scale species richness patterns are driven by diversity dynamics within relatively independent biogeographic units ('evolutionary arenas' *sensu* Jetz & Fine 2012) whose diversity is determined by evolutionary rates of speciation and extinction (Rosenzweig 1995). In contrast, local communities represent samples within those large units, whose diversity depends also on migration from neighbouring communities so that the links between E, J and S revealed by the theory below are confounded by homogenising effect of colonisation (see Supporting Information). The theory is based on the following considerations which can be expressed mathematically (Fig. 6):

(1) Species-specific rates of speciation and extinction are dependent on population size, N, that is, there are particular functions relating the probabilities that species go extinct and speciate to their population sizes. We assume that extinction probability is a decreasing function of population size N (Fig. 6c), while speciation probability is likely either independent of N or is an increasing (or potentially also decreasing, see Fig. 5) function of N (Fig. 6a). These functions are additionally affected by the properties of environment, for example, the extinction function reflects environmental stability (as extinctions are less likely in more stable environments).

(2) The probability distribution of species population sizes N within a community (the species-abundance distribution, SAD) is characterised by a specific function. Recognising that the SAD can be driven by multifarious interacting effects (Pueyo 2006; Pueyo *et al.* 2007), it is safer not to model it by a specific mechanism. Since the log-series distribution is predicted by the neutral theory of biodiversity (Hubbell 2001), maximum entropy theory of ecology (Harte *et al.* 2008) and idiosyncratic theory of biodiversity (Pueyo *et al.* 2007), and is empirically well supported (Baldridge *et al.* 2016), we use the log-series SAD in the illustrative implementation of our theory (Fig. 6b), but many general predictions can be made without assuming a particular form of the SAD (see Figs. 6e and 7).

(3) The total number of individuals J is affected by the collective capacity of species to utilise available energy. *Maximum* sustainable J is limited by the maximum possible rate of flux of energy E available to the community and mean individual metabolic rate B, so that $J_{max} = E/B$. This follows from bioenergetic principles dictating that individuals must obtain enough energy to meet metabolic requirements for maintenance, growth and reproduction (Brown *et al.* 2004). This axiom is the simplest mechanism linking E to J and is implicit to most of the MIH literature. Additionally, since different species have different ways of utilising resources, with the addition of new species, there is a higher probability that some otherwise under-utilised resources is used. Consequently, all else being equal, a more species-rich community utilises a greater proportion of E, leading to J being a plateauing function of S, whose maximum is constrained by E/B and dependence of J on S reflects resource diversity, interspecific packing of resource utilisation niches and effect of S on resource use by the community, such as due to facilitation (Fig. 6d). Note that E is simply the external input of utilisable energy into given community regardless of whether it is driven by abiotic or biotic factors (which may reveal historical legacies).

(4) In a given time interval, each species in a community may go extinct or speciate with a probability determined by their speciation and extinction functions. Total extinction and speciation rates are then the aggregation of extinction and speciation probabilities, respectively, across all species. How J and S interact with the SAD and extinction and speciation functions can be resolved mathematically and thus when diversity hovers around equilibrium, relationships between S, J and speciation and extinction parameters can be predicted (Fig. 6e and Supporting Information). Our framework can thus provide predictions for how resource supply interacts with environmental drivers of speciation, extinction or resource utilisation, producing predictable patterns in S, J and mean abundance (Fig. 7).

We assume that any emergent effects of species interactions can be encapsulated by the four functions in Fig. 6 and that parameters of these functions are independent of each other. We emphasise that this theoretical framework does not need to assume that species are equal in their access to resources nor that habitat heterogeneity or niche differences are unimportant. To the contrary, it is designed to address situations in which not all species compete for the same resources or habitats. However, even though species may specialise on different resources, the energy available to an ecological system sets an upper limit on the maximum total metabolism and number of individuals of a community. Consequently, as niches and habitats become increasingly filled with increasing S, the community's use of resources approaches the total energy available and thus the addition of species must lead to some level of resource niche overlap, eventually leading to a

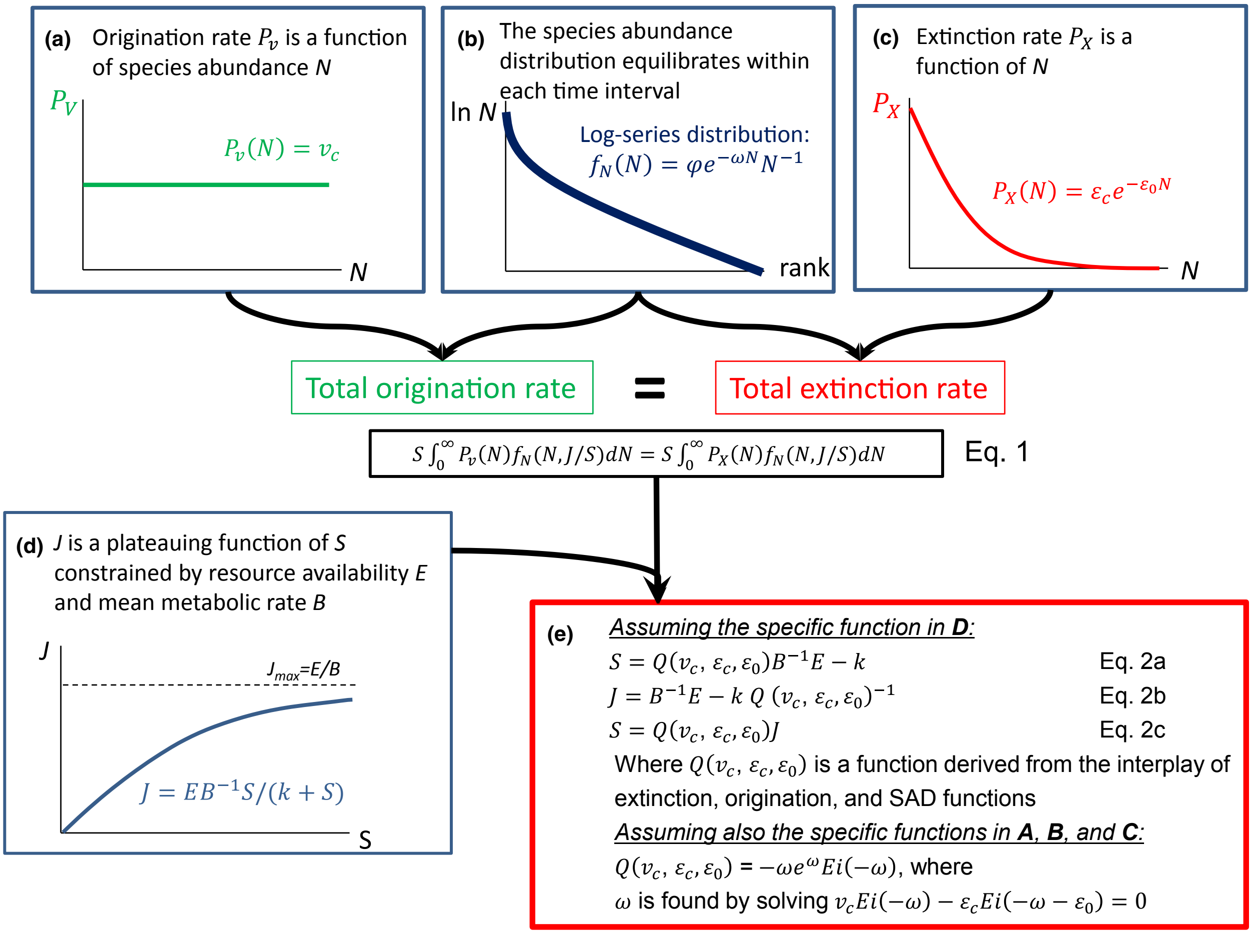


Figure 6 Core components of the theory of diversity dynamics and demonstration of how their interplay at large spatial scales determines functional relationships between species richness *S*, total number of individuals *J*, resource availability *E* and properties of extinction, speciation and the overlap in resource utilisation niches (for details see Supporting Information). The specific functions are shown as examples and are not essential for the general predictions made in Fig. 7 that apply to large biogeographic scales. The total rates of speciation and extinction in a community are the summation of the number of taxa originating and going extinct in each abundance class within a time interval, which reflects the interaction of the species-abundance distribution's density function f_N (see b) with the functions describing how the proportions of taxa of abundance *N* that speciate (P_V, see a) and go extinct (P_X, see c) change as a function of *N*, as shown in eqn 1. If resources are diverse, then low-diversity communities may lack species with the appropriate niches in order to fully utilise all available resources (non-horizontal line in d) and increasing *S* (through increased speciation or decreased extinction) increases community resource use and *J* up until the community is using all available resources (fully 'saturated' and energetically constrained). Integrating eqn 1 and taking into consideration the effects encapsulated by the function in d, it follows that at equilibrium proportionality between *S* and *E* is only expected in saturated communities (eqn 2a) but *S* should indeed change proportionally with *J* in all community types, as long as there is limited variation in properties and parameters of the SAD, speciation, and extinction functions (eqn 2c). So, the interactions between the functions in d, a, b and c and the degree to which different variables are varying determine the relationships between equilibrium S, *J*, *E* and parameters related to extinction, speciation and resource utilisation niche structure (e). In addition to specific predictions using particular functions, general predictions regarding the relationships between *S*, *J* and *E* can also be made that assume very little about the functions.

decline in populations of other species in order to accomodate the additional species. This effect may be indirect, such as when folivory's damage to a tree reduces the production of seeds consumed by seed-eaters. Habitat heterogeneity may modulate these various processes, although its role is complex, since heterogeneity can increase probabilities of species coexistence but also leads to smaller areas of individual habitats, which may increase probabilities of extinction (Allouche *et al.* 2012). Our framework's purpose is not to explicitly model these intricacies, since the emergent effects of these complex dynamics are reflected by respective extinction and speciation functions (Fig. 6). Similarly, our theory also implicitly incorporates the effects of environmental stability. The area and productivity of biomes can vary considerably through time (see Jetz & Fine 2012), which some researchers have considered as indicating that communities are not at equilibrium. However, such environmental changes can instead be taken as variables affecting equilibrium dynamics through their effect on species extinction rates at large temporal scales.

Although application of the framework to make very precise predictions requires assuming particular functions (Fig. 6's eqn. 2), there are coarse-grained quantitative predictions and conclusions concerning large biogeographic scales, such as the latitudinal diversity gradient (Figs. 6 and 7). Not

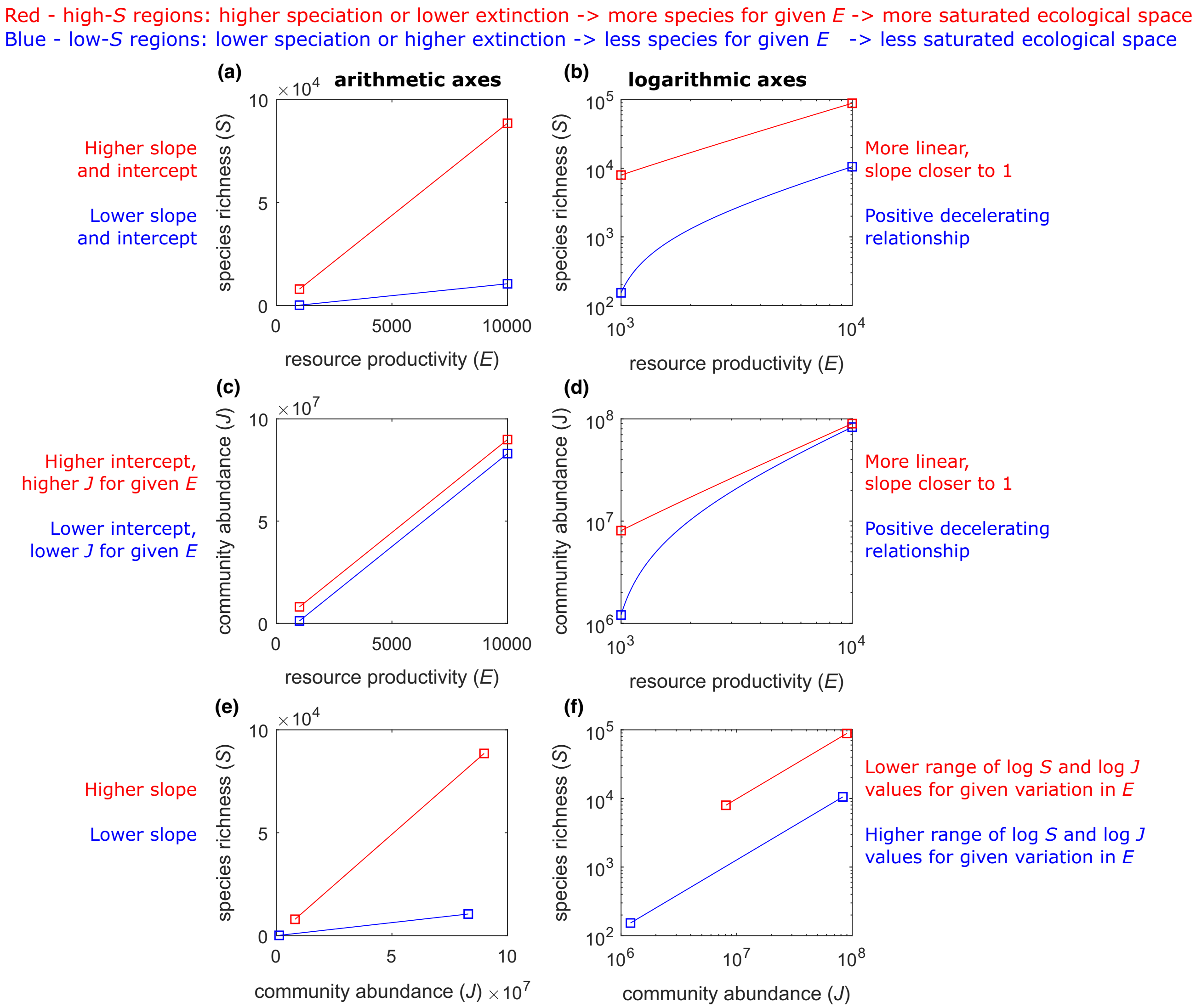


Figure 7 Unique predictions of the theory for large biogeographic scales. The theory provides contrasting predictions concerning the relationships between E, J and S, for environments characterised by high probabilities of speciation and/or low probabilities of extinction (e.g. stable warm environments like the tropics; red; hereafter high-S environments) versus environments characterised by low speciation and/or high extinction probabilities (e.g. unstable cold environments, like the temperate zone; blue; hereafter low-S environments). For a given level of energy availability, the high-S environment compared to the low-S environment is more species-rich, and the relationship between S and E has a higher slope in arithmetic axes (a), is closer to approximating proportionality, and exhibits increased linearity in logarithmic axes (b). Lower species richness in low-S environment leads to relatively lower community abundances J for given energy availability (c), as the lower number of species less effectively utilises available resources; therefore, it is in a sense unsaturated, which is reflected in more apparent decelerating relationship between both E and S (b) and E and J (d) on logarithmic scales. Also, the theory predicts proportionality between J and S regardless of the level of saturation of the community as long as variation in parameters of extinction, speciation and the SAD is limited and invariant of E; however, the high-S environment is predicted to reveal higher species richness and higher slope of the J–S relationship in arithmetic axes (e), and lower variation of abundance in the log scale (f). Plots here show curves for the specific functions described in Fig. 6, using illustrative parameter values.

surprisingly, the theory shows that equilibrium species richness is predicted to increase with: (1) decreases in the parameters that augment extinction (e.g. environmental stochasticity), (2) increases in the speciation probability parameter ν_c, (3) increases in energy availability E, (4) decreases in individual metabolic rate B, (5) increases in the ability of species to utilise available resources, as captured by lower values of the parameter k in Fig. 6d. In Fig. 7, we provide some examples of more nuanced predictions that can be made concerning the relationships between energy (or resource) availability, abundance patterns and species richness.

IMPLICATIONS OF THE FRAMEWORK OF EQUILIBRIUM DYNAMICS FOR PREVIOUS AND FUTURE MIH TESTING

Our theoretical framework can be applied to evaluate predictions that have been used for testing the MIH (Figs 1 and 3c). In this context, it is useful to distinguish between: (1) the strict formulation of the MIH, which is most typical in the literature and states that species richness variation is driven just by variation of E through its effect on J; and (2) a soft formulation of the MIH stating that J is involved in species richness regulation, although the other effects (e.g. environmental stochasticity or colonisation and speciation rates) may also participate in generating patterns in S.

At small spatial scales, migration likely masks the dependence of S on J, leading to a nonlinear and potentially quite weak relationship between these variables (see Supporting Information). In contrast, at larger spatial scales comprising relatively independent units with largely separate evolution, our theory makes several general predictions (Fig. 6e). When parameters of species origination, extinction and SAD are constant, increasing J in the community by increasing E should lead to a proportionate increase in S, and also E, J and S should be positively correlated with each other. This is in accord with predictions 1–3 from Fig. 3. So, if these predictions do not hold (as is sometimes the case, see Fig. 3), then either (1) other effects must play a role and the strict version of the MIH can be rejected; or (2) the spatial scale was not well suited for the MIH tests and the patterns were masked by migration. However, if they do hold, it does not violate the possibility that the other factors play some role.

A bit more problematic is prediction 4 stating that under the strict formulation of the MIH, the S–E relationship should be weaker than both J–E and S–J relationships. Since our theory predicts that the S–J relationship shares fewer parameters than the J–E and S–E relationships and log J's range of values ≥ log E's range of values, the S–J relationship is indeed expected to be stronger than the S-E relationship and also most likely stronger than the J–E relationship. These two relationships are affected by incomplete species niche overlap and effectiveness of utilising resources, and thus even the J–E relationship can be relatively weak according to our theory. Therefore, the finding that the S–J correlation is weaker than the S–E correlation can be taken as a valid argument for rejecting the strictly formulated MIH (Currie *et al.* 2004), keeping in mind, however, that the test may be problematic if only a small range in E is examined or if measurement error is higher for abundance than species richness or productivity data.

Some other predictions that have been used to test the MIH in fact do not follow from its strict formulation. Because all else being equal S is predicted to be proportional to J across large regions, mean species abundance is expected to be invariant in respect to changing J. Therefore, there is no reason for the prediction that mean population size is positively correlated with E and S (prediction 5 from Fig. 3). Consequently, since the strict version of the MIH assumes that extinction rate is driven only by population size, it predicts also invariant per-species extinction rates with changing energy availability, and thus prediction 7 in Fig. 3 also does not follow from the strict MIH. Moreover, if migration plays a role, sublinear J–S scaling is predicted (Supplementary Information), so that mean population sizes are expected to *decrease* with increasing E and J. Similar reasoning applies for all the remaining predictions – they do not follow from the strict formulation of the MIH and observing predicted patterns (such as the positive relationship between energy availability and mean population size) instead indicates that some other processes besides E and J are affecting the variation in diversity.

Our theoretical framework thus indicates that while empirical support for the first four predictions from Fig. 3 can lend indirect, weak support to both the strict and soft MIH, only predictions 3 and 4 can be used to reject the strict MIH – the strict MIH is rejected when S is not proportional to J or when the S–J relationship is weaker than the S–E relationship. In light of our derivations, the published empirical evaluations of the first four predictions provide mixed support for the strict MIH (Figs 1 and 3), indicating that in many cases other factors very probably play a role in generating spatial variation in diversity. However, none of the reviewed literature predictions can be used to evaluate the soft formulation of the MIH, that is, to reject the possibility that the total number of individuals is crucial to diversity *regulation* even when variation in other eco-evolutionary processes underpin observed *variation* in diversity. The reason is that the exact nature, strength and variability in the other processes participating in diversity regulation of communities can obfuscate the role of J and thereby hinder correlational evaluations of the underlying role of J.

One way to disentangle these interlinked factors would comprise simultaneous evaluation of all the effects that presumably participate in diversity dynamics, namely resource abundance, environmental fluctuation and temperature (presumably affecting speciation rates; Allen *et al.* 2006), for instance using structural equation models (Grace *et al.* 2010, 2014). The theory also provides some unique predictions which enable further testing (Fig. 7). For instance, it predicts that in environments with increased extinction or reduced speciation rates, species richness should increase more disproportionately with E, exhibiting a more curvilinear, decelerating relationship between log S and log E than in low extinction or high speciation environments.

DISCUSSION AND PERSPECTIVES

The more-individuals hypothesis has been considered the most straightforward explanation of observed species–energy relationships (Gaston 2000), but various tests only rarely provided conclusive support of it. This is partly the result of the MIH having not been properly and sufficiently formalised, so that it has not been clear what quantitative predictions should actually be tested. The only exception is the sampling effect, which can be easily simulated if the total sample size (total number of individuals and species within a larger region) is known together with a species-abundance distribution. However, this may be relevant only at small spatial scales in which local communities can be modelled as subsamples of large regions (Gaston & Blackburn 2000). At large scales, diversity as well as abundances result from particular dynamics.

We have provided a general characterisation of such dynamics which includes a negative diversity dependence mediated by diversity-dependent population sizes with consequent extinction dynamics. We argue that this framework encompasses the essential features of the majority of models of biodiversity dynamics at large scales, and provides pathways for more rigorous evaluation of the roles that community abundance has in regulating species richness patterns. Some of the tests performed by various authors are inappropriate in the light of this dynamics, as they concern patterns which do not represent any reasonable predictions following from the dynamics. Other tests can evaluate if the species richness variation is driven by variation in E or J, but they cannot shed light on the overall role of J when species richness is affected by combination of several interacting factors that can obfuscate the role of J. The MIH can be therefore mostly rejected in its strict formulation, that is, the statement that energy-related diversity variation is driven *only* by the variation in the amount of resources that constrains the total number of individuals able to persist in an environment. In contrast, the statement that resource level or community abundance participates in diversity *regulation* could not be rejected.

This means that further research should not be devoted to testing the MIH in isolation. Instead we advocate testing all the major potential effects together using a well-developed theoretical framework. We have shown, using our theory, that the soft formulation of the MIH (that assumes that total number of individuals is involved in species richness regulation) leads to non-trivial predictions concerning different relationships between E, J and S, in the environments differing in the overall level of speciation and/or extinction (see Fig. 7). These rates can be independently evaluated using some proxy data on the past effects of these variables. Statistical tests guided by the theory can also be used to disentangle the interacting effects of resource levels and environmental stochasticity on total extinction rates and species richness using biogeographic gradients in which these variables exhibit limited co-variation. Additionally, it will be useful to build versatile simulation models of biodiversity dynamics (such as those in Hurlbert & Stegen 2014a,b) that would not rely on an assumption of species demographic equivalence, in order to address the whole range of basic process outputs that can be expected under different scenarios of community assembly and diversity regulation. Last but not least, the validity of the equilibrium assumption will need to be explored in a variety of environments, taxa and time periods.

The processes behind spatial species richness patterns are still enigmatic. Although many currently favour historical explanations for large-scale spatial richness variation such as the latitudinal diversity gradient – with high species richness argued to be associated with old and stable environments, which allowed more lineages to originate and adapt (e.g. Kozak & Wiens 2012) – current findings concerning the independence of many of such richness patterns from particular histories of colonisation and diversification (Belmaker & Jetz 2015; Hawkins *et al.* 2012; Oliveira *et al.* 2016) indicate that the current environment sets up some attractors for particular richness values. Correlation of species richness with various measures of energy availability provides good reasons to believe that population size-mediated extinction dynamics lies behind the patterns, but since energy availability often covaries with other environmental variables, the spectrum of potential processes is much wider. Moreover, since extinction dynamics is certainly affected by environmental stability, and species richness is certainly affected also by colonisation and speciation, there is no reason to assume that only one process determines the observed species richness patterns. Still, it is crucial to reveal the role of available energy in comparison to other factors in generating diversity patterns (e.g. as in Okie *et al.* 2015). In the era of the Anthropocene, a considerable proportion of primary productivity is appropriated by human populations (Haberl *et al.* 2007) and changing temperature, nutrient conditions and precipitation regimes are altering the abundance and production of many communities (Rosenzweig *et al.* 2007; Walther 2010). Knowledge of the causal relationship between energy availability and biodiversity is thus essential for predicting future biodiversity changes (Miko & Storch 2015).

In summary, we have shown that published tests of the MIH do not provide strong support for the strict version of the MIH – in many cases, species richness variation was not driven by energy-related variation in total number of individuals. However, since the MIH was not well formalised, tests of the MIH did not conclusively reveal the extent to which the energy-related total number of individuals participates in the *regulation* of the equilibrium number of species, as hypothesised by the soft formulation of the MIH. Although other effects, including environmental stability and various drivers of speciation or colonisation, are probably more important for generating many spatial diversity patterns, such as the latitudinal diversity gradient, the effect of energy availability on total abundances is probably still an important factor underpinning many spatial and temporal diversity patterns due to its effect on diversity-dependent extinction rates.

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AUTHORSHIP

D.S., E.B. and J.O. conceived the study; D.S. and E.B. reviewed and evaluated all the published studies; D.S. and J.O. developed the presented formal framework; D.S., J.O. and E.B. wrote the manuscript.

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Additional Supporting Information may be found online in the supporting information tab for this article.

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