Title: Macroecological rules predict how biomass scales with species richness in nature

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Abstract: Despite advances in theory and experiments, how biodiversity influences the structure and functioning of natural ecosystems remains debated. By applying new theory to data on 84,695 plant, animal and protist assemblages we show that the general positive effect of species richness on stocks of biomass, as well as much of the variation in the strength and sign of this effect, is predicted by a fundamental macroecological quantity: the scaling of species abundance with body mass. Standing biomass increases with richness when large-bodied species are numerically rare but is independent of richness when species size and abundance are uncoupled. These results suggest a new fundamental law in the structure of ecological communities and show that the impacts of changes in species richness on biomass are predictable.

Main Text: Human activities are rapidly eroding global biodiversity, creating a pressing need to understand the consequences of these losses for the structure and function of Earth's ecosystems (*1-3*). Hundreds of experimental studies based on artificial species assemblages have provided critical evidence that biodiversity supports higher standing stocks of biomass and fluxes of energy through ecosystems (*4*), and theory identifies several underlying mechanisms for these effects (*5-7*). But understanding the relationship between biodiversity and the structure and functioning of assemblages in nature, with their greater scale and complexity, remains a major challenge (*8*).

On the one hand, many empirical studies of animal and plant assemblages have reported positive associations between species richness and biomass that are consistent with, or stronger than, effects estimated from experiments (*9-11*). However, in other cases, the biomass supported by an ecosystem appears to be decoupled from changes in species richness, or even declines at higher levels of biodiversity (*11-13*). This heterogeneity has led to the suggestion that the effect of species richness on ecosystem function in nature is likely to be idiosyncratic and context dependent, eluding a general unifying theory (*14*). The problem is therefore to explain not only the widespread empirical trend for biomass stocks to increase with biodiversity, but also the substantial variation in the strength and sign of this relationship (*15*). In contrast to artificial species assemblages, which typically consist of random mixtures of species, natural assemblages exhibit a number of general regularities, or 'macroecological rules', that describe how the abundance of individuals and their traits—such as body size—are distributed across species and space (*16, 17*). One potentially promising approach for understanding the effect of biodiversity on ecosystem functioning is therefore to consider the patterns that arise from the macroecological rules governing how assemblages in nature are structured (*18*).

Here we develop and test a macroecological model to predict the effect of species richness on standing biomass. While biomass represents a simplistic proxy that does not capture the full multi-dimensional nature of ecosystem functioning (*19*), we use it here because it provides a universal and widely measured property of ecosystems linked to a variety of critical functions and services (*13*), including carbon storage (*20*), primary production (*21*) and trophic energy flows (*22*). Our model is designed to make minimal assumptions while capturing the key macroecological rules that describe how assemblages in nature are structured and sampled. These rules should be applicable to any kind of organism or environment (*23*) and thus we assess the predictions of this model using data on the richness and standing biomass of a diverse compilation of aquatic and terrestrial assemblages spanning plants, animals and protists (Table S1). Our analysis reveals how the general positive effect of species richness on stocks of biomass observed across taxa arises from a well-known but previously unlinked macroecological rule: the trend for large bodied species to be numerically rare.

A macroecological model of biomass scaling with species richness

To understand the link between biodiversity effects, species abundance and body size, consider a model consisting of a regional pool of species that vary in their abundance (A) and body mass (M) (Fig. 1) (*24*). We assume that variation in species body masses and abundances both follow the widely supported lognormal distribution (*17, 25, 26*) and that, as is common in nature, A and M are negatively related (*27, 28*) and follow a power-law relationship with exponent λ. That is, when plotted on a log-log scale this relationship is linear with slope λ.

$$log(A) = constant + \lambda \times log(M)$$

Such a negative effect of M on A is often attributed to energetic or spatial constraints on population carrying capacity, as larger organisms that consume more resources and occur at higher trophic levels can be supported at lower densities (*28-30*).

Further assume for simplicity that local assemblages represent random samples of individuals drawn from the environment. Differences in richness and biomass across assemblages thus arise in our model due to stochastic variation in the sampled abundance of each species. A positive relationship between species richness and biomass in our model could arise because species rich assemblages (*i*) contain a greater number of individuals and/or (*ii*) contain individuals which are on average larger, with these having potentially different implications for ecosystem functioning (*31*). Because the effect of the number of individuals is relatively straightforward, we focus on the average size effect, by examining the relationship between species richness and biomass across samples of a fixed total abundance. We later relax this assumption to explore the joint effect of the number of individuals and average size. We focus on predicting the slope (θ) of the least squares regression of log-log transformed biomass (B) on richness (R).

$$log(B) = constant + \theta \times log(R)$$

Our use of a power law to estimate θ should not be taken to imply we are assuming a particular mechanistic basis to this relationship, or that this is necessarily the best fitting model. Rather we follow previous broad-scale analyses (e.g., (*32*)) in using a power law because we are interested in predicting the relative change in biomass given a relative change in species richness, allowing comparison across organism groups where body mass is measured on very different scales.

This simple theoretical model reveals that a positive effect of species richness on standing biomass ($\theta > 0$) arises due to the general macroecological rule for abundance to decline with body mass ($\lambda < 0$) (Fig. 1). First, note that when a constant number of individuals is repeatedly sampled at random from the species pool, variation in richness and biomass is mathematically constrained. Assemblages that, by chance, contain only a single species can have anything from a very low to very high total biomass, depending on whether the individuals come from the smallest- or largest-bodied species respectively. In contrast, a species-rich assemblage must contain both small- and large-bodied species (because there are a limited number of small-bodied and large-bodied species, respectively, to sample from) and is thus constrained to have an intermediate biomass. Second, note that while this mathematical constraint defines the space of possible richness and biomass values, assemblages are unlikely to occupy this space evenly. This is because when individuals are randomly sampled from the environment, small-bodied species that occur at a higher abundance are more likely to be included in the sample. Thus, for an assemblage where, by chance, all individuals that were sampled happened to belong to a single species, it is much more likely to be a common small-bodied species than a rare large-bodied species. This dominance of small individuals will result in this species-poor assemblage having a relatively low standing biomass. Equally, the rarity of large-bodied species makes them less likely to be sampled, and these rare species will tend to only be represented in those assemblages that by chance have a higher species richness. The presence of these rare but large-bodied species ensures a relatively high standing biomass in species-rich assemblages compared to assemblages comprising fewer species. Thus, when large-bodied species are numerically rare (λ

< 0), the random sampling of individuals alone can generate a positive relationship between species richness and biomass (θ > 0).

While it has been argued that the species body mass-abundance relationship has a canonical form of $\lambda = -3/4$ (*26*), empirical studies show that λ varies across taxa and contexts from strongly negative to absent or even weakly positive (*27*). We therefore next examined the effects of variation in λ on the expected slope of the richness-biomass relationship. Throughout our theoretical analysis, we use the value of λ estimated from the abundance of species across the simulated local assemblages matching the kind of data typically available in empirical studies. We note, however, that similar theoretical results are obtained when using the body mass-abundance relationship of the regional pool (fig. S1).

Our macroecological model shows that variation in λ is expected to give rise to predictable variation in the sign and strength of θ (Fig. 2A). Specifically, when body mass is negatively correlated with abundance (λ < 0), then as illustrated in Fig. 1, the expected effect of richness on biomass is positive (θ > 0). In contrast, when variation in species body mass and abundance are independent (λ = 0), biomass is expected to vary independently of species richness (θ = 0). And, when the typical relationship between species body mass and abundance is reversed—so that numerically abundant species have a larger body mass (λ > 0)—the expected effect of richness on biomass is also reversed, with biomass declining with increasing richness (θ < 0).

While λ acts as a master variable controlling the sign of θ, our simulations show that it explains only limited variation in the magnitude of θ, as this also depends on the variance in log-transformed M ($\sigma^2_{log(M)}$) and A ($\sigma^2_{log(A)}$) (Fig. 2A). When there is relatively little variation in body mass among species, then regardless of how these species are mixed within assemblages, total biomass will vary little. When there is relatively high variation in abundance among species, most assemblages will comprise the same highly abundant species, again resulting in little variation in biomass. Thus, for a given λ, the expected magnitude of θ can vary substantially (Fig. 2A). Rescaling λ by the relative variance in log-transformed M ($\sigma^2_{log(M)}$) and A ($\sigma^2_{log(A)}$) provides a metric, λ_S, that accounts for these effects.

$$\lambda_S = \lambda \times \frac{\sigma^2_{log(M)}}{\sigma^2_{log(A)}}$$

Having done this rescaling, the unexplained variation in θ largely collapses, with λ_S reliably predicting both the expected sign and steepness of θ (Fig. 2B). An exact analytical link between θ and λ_S is lacking and the exact form of the relationship depends on the precise parameters of the model, such as the number of species in the regional pool (figs. S2-S3). However, sensitivity analyses suggest that under a range of realistic scenarios, λ_S could serve as a heuristic metric to predict how changes in species richness influence the biomass of ecological assemblages (*24*). For example, the strong theoretical dependency of θ on λ_S is robust to relaxing key assumptions of our model, including the shape of the species abundance distribution (fig. S3), the presence of intra-specific size variation (fig. S4) and non-random sampling arising due to the spatial aggregation of species populations (figs. S5-S6). When we relaxed our assumption that assemblages consist of a fixed number of individuals, we continue to observe a strong dependency of θ on λ_S (Fig. 2c). In this case, and for a given value of λ_S, the expected slope of the richness-biomass relationship is shifted upwards and is consistently positive, because assemblages containing more individuals will tend to sample more species and to contain a higher total biomass (fig. S7). This effect becomes progressively stronger with increasing variation in the number of individuals across assemblages, until eventually (e.g., with 20-fold variation in total abundance) θ is strongly positive regardless of λ_S (Fig. 2c). Taken together, these results confirm the strong theoretical dependency of the richness-biomass relationship on the number of individuals, while revealing an additional macroecological rule, whereby differences in λ_S modulate the richness-biomass relationship by altering the average body size of the individuals in an assemblage.

Biomass scaling with species richness across taxa in nature

To test this theoretical prediction, we collated a database of assemblages comprising records of species abundance across multiple survey sites and for which we could obtain estimates of individual or species average mass (*24*). In total, our database includes 84,695 assemblages, consisting of ~60 million individual organisms and 4,092 species. Those species come from 11 major taxonomic groups with vastly different ecologies, from earthworms to elephants and from unicellular nanoplankton weighing one trillionth of a gram to trees weighing 200 tonnes (Table S1). The empirical relationship between richness and biomass could be sensitive to difference in the area or volume (i.e., grain size) of survey sites, as larger grains will encompass more habitats and individuals (*33*). While grain size necessarily varies substantially across organism groups, we selected datasets such that within each group assemblages were generally sampled using a standardised grain size that reflects the relevant scale at which those individuals within that group interact. Nevertheless, the number of sampled individuals often varied substantially across assemblages driving consistently strong positive richness-biomass relationships (fig. S8, table S2). Variation in the number of individuals across empirical assemblages could reflect a causal effect of biodiversity on organism density (*31*). However, as predicted by our theoretical model, it could also reflect the stochastic nature of sampling (*24*) or environmental (e.g., energetic (*34*)) constraints on carrying capacity, both of which could drive the appearance of a positive effect of richness on biomass. To isolate the effect of richness on biomass independent of total assemblage abundance, we therefore subsampled (i.e., rarefied) assemblages to a constant number of individuals before estimating biomass, richness and θ (*24*).

Across most taxa, stocks of biomass increase with species richness, supporting the widely reported positive effect of biodiversity on biomass (*11*). However, θ varies substantially across groups (Fig. 3A): it is significantly positive for six of the eleven taxonomic groups, is not significantly different from zero for three (mammals, earthworms and coccolithophores) and for two others is significantly negative (moths and birds) (table S3). This is consistent with the heterogeneity in the effects of biodiversity on biomass previously reported for natural assemblages of animals and plants (*11-13*). In accordance with our theoretical model, much of this variation in the sign and steepness of θ across these taxonomic groups follows predictably from variation in the sign and magnitude of λ_S that we estimated from our raw local assemblage data (i.e., prior to rarefaction) (Fig. 3C). For example, fish exhibit the steepest negative λ_S ($\lambda_S =$ -0.29) and accordingly also exhibit the steepest increase in biomass with species richness. In contrast, λ_S is weakly positive in our dataset of UK breeding birds (λ_S = 0.04), and in this group biomass declines with species richness. Other groups have intermediate values of λ_S between these extremes, with the effect of species richness on biomass varying as predicted i.e., becoming more strongly positive as the effect of body size on abundance becomes more strongly negative (table S3).

Overall, a linear model including λ_S alone is able to explain 60% of the variation in θ across taxonomic groups (intercept = -0.02, slope = -2.58, p = 0.003 (*24*)). This strong dependency and predictive power is robust to uncertainty in estimates of $\lambda_S$and θ, including that resulting from how assemblages are subsampled (figs. S9-10) and whether they are standardised to a constant abundance or level of sampling completeness (fig. S11). Variation among taxonomic groups in θ is also predicted by the unscaled slope λ (intercept = 0.08, slope = -0.88, p = 0.03, r^2 = 36%), but in accordance with our theoretical model, this dependency is weaker than the dependency on λ_S (Fig. 3B). Examples from particular taxa highlight the reason for this. For instance, species abundance in Dinoflagellates declines strongly with size (λ = -0.56), but because there is relatively little variation in body mass among species, θ is weaker than expected from λ alone. In contrast, fish exhibit relatively large variation in body mass and this, combined with the strong negative scaling of abundance with size (λ = -0.47), results in a particularly steep increase in biomass with species richness. Richness-biomass relationships are thus most steeply positive in those taxa that exhibit both strong size-dependent constraints on abundance and substantial variation in body mass across species.

Conclusions

Together, our theoretical and empirical findings provide evidence that the general positive effect of species richness on the standing biomass of natural assemblages across ecosystems arises as a mirror image of the general negative effect of body mass on species abundance within ecosystems. Furthermore, far from being idiosyncratic, we show that differences among taxa and environments in the sensitivity of biomass to changes in species richness arise predictably from differences in the scaling of abundance with body size. For example, biomass increases more strongly with species richness in aquatic compared to terrestrial groups (*32*), as expected from the stronger negative scaling of abundance with body size in aquatic ecosystems (*35*). While in this work we have focussed on comparing organism groups with very different size structures, we note that human activities have driven, and continue to drive, profound changes in the distribution of species size and abundance (*36*, *37*). Our model could provide a basis for predicting the consequences of these changes in size-structure for how biodiversity influences ecosystem function.

Our results should not be taken to suggest a simple bivariate relationship between richness and biomass in nature, and its dependency on the species body mass-abundance slope. As we show, uncovering these relationships requires first controlling for differences in the relative extent of variation in body mass across species (Fig. 2B) and for differences across assemblages in the number of individuals (Fig. 2C). An important next step will be to integrate our findings into a more general theoretical framework that aims to predict these additional state variables that are critical for a comprehensive understanding of how biodiversity and ecosystem function are connected (e.g., (*18*, *34*)). Further work is also required to understand how different regional pool structures, environmental contexts, non-random patterns of sampling and community assembly processes—including interactions between species—alter our theoretical predictions and ability to explain the empirical patterns. For example, the key ecological mechanisms of niche complementarity and facilitation that experiments have shown promote higher biomass in more species rich systems (*6*) are not explicitly considered in our model. Incorporating these mechanisms could potentially explain additional variation in the richness-biomass relationship, especially for organisms where body size varies substantially within species (e.g. trees) (*24*).

The ability of our model to predict how biomass scales with species richness without considering niche complementarity or facilitation should not be taken to imply that these mechanisms are unimportant in explaining patterns of ecosystem functioning in nature. Rather, our results suggest that knowledge of how these mechanisms operate may not be required to predict the impact of changes in species richness on biomass (*38*). For example, the key constraint identified in our theoretical model that drives increases in biomass with species richness, is for numerically rare (large bodied) species to preferentially occur in more species rich assemblages (Fig. 1). In our model this arises due to random sampling, but the same effect could be driven by other niche-based mechanisms that cause numerically rare species to congregate in the richest assemblages (e.g., lower extinction rates) (*34*). Our analysis is unable to resolve what ultimately drives the distribution of rarity across species assemblages and body size classes (*27*), but the quest to identify the causes of these macroecological rules (*39*) emerges from our analysis as a priority for understanding the role of biodiversity in the functioning of ecosystems.

Here we identify a previously unappreciated fundamental law in the scaling of biomass with species richness that appears to hold across contrasting physical environments and kingdoms of life. Because metabolic rates and fluxes of energy and matter consistently scale with body mass (*40*), and because abundance covaries with a number of other species traits (*41*), this law could encompass similar generalities in the relationship between other facets of biodiversity (e.g. functional trait diversity) and metrics of ecosystem function (e.g. productivity or stability). Such a prospect points towards a unification of macroecology and ecosystem science, in which changes in the structure and functioning of ecosystems can be predicted from the natural rules governing the abundance and distribution of individual species.

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Data and materials availability: Data and code to reproduce the analysis is available at (*42*). The moth data used in the analysis are openly available in the Rothamsted Repository at (*43*). In (*42, 43*), moth and bird species and location names are anonymised. The original data for moths and birds is available on request from the Rothamsted Insect Survey (RIS) and The UK Breeding Bird Survey.

Supplementary Materials

Materials and Methods

Figs. S1 to S14

Tables S1 to S7

References (*44–80*)

Fig. 1. How size-dependent constraints on species abundance determine the effect of richness on biomass stocks. (A) Within a regional pool of species, species abundance (*A*) varies inversely with mean species body mass (*M*) (here, $\lambda = -1$). For simplicity here we show a species pool consisting of 5 hypothetical species represented by circles of different colors, with circle size denoting mass *M*. **(B)** A fixed number of individuals (here $n = 5$) are repeatedly drawn at random from the species pool to form local assemblages, which exhibit stochastic variation in both richness and biomass. Here three exemplar assemblages are shown. While not evident in this simplified example with only five individuals, local assemblages exhibit species body mass-abundance relationships mirroring the regional pool (fig. S1). **(C)** The two-dimensional space of all possible richness (*R*) and biomass (*B*) states from our model are constrained (dashed black lines) by the body masses available in the species pool. Cells indicate the probability (dark shading indicates higher probability) of each richness-biomass combination under a random draw of individuals. Solid line shows the expected effect of species richness on biomass (θ) estimated via least squares regression. For each level of species richness, assemblages with the highest and lowest possible biomass are shown. Numerals indicate the richness-biomass states of the assemblages shown in (**B**). For simplicity in this example, intraspecific size variation is ignored, but the dependency of θ on λ is robust to intraspecific size variability (*24*).

Fig. 2. Theoretical expectation of how differences in size-dependent constraints on species abundance drive heterogeneity in the sign and steepness of the species richness-biomass relationship (θ). (A) The slope λ of the relationship between species body-mass (*M*) and abundance (*A*) determines the expected sign of θ. For a given λ, the steepness of θ varies widely depending on the relative variance in species body mass ($\sigma^2_{log(M)}$) and species abundance ($\sigma^2_{log(A)}$), indicated by different colors. Each point shows the mean θ across 500 replicate simulations. **(B)** When accounting for the variance in body mass and abundance, the rescaled species body-mass abundance relationship λ_S strongly predicts both the sign and steepness of θ. **(C)** the dependency of θ on λ_S when the total number of individuals varies across assemblages, showing scenarios from a 2-fold to 20-fold variation in total abundance. In (**A-C**) λ and λ_S are estimated from the species abundance across local assemblages to match the empirical data typically available.

Fig. 3. Size-dependent constraints on species abundance predict heterogeneity in the slope of the species richness-biomass relationship (θ) across taxa. (A) The observed relationship for each taxonomic group ($n = 11$) between log-log transformed species richness and biomass and log-log transformed species body mass and abundance. Lines are estimated regression slopes (table S3). Groups are ordered according to the rescaled species body-mass abundance relationship λ_S, from steeply negative (left) to positive (right). **(B)** Covariation across taxonomic groups between the slope of the species richness-biomass relationship (θ) and the slope of the relationship between species body-mass and abundance (λ) (**C**) Covariation between θ and λ_S, the rescaled slope of the relationship between species body-mass and abundance. In (**B, C**), colors indicate the taxonomic group in (**A**). Bars show 95% confidence intervals (not visible for some taxa). The fitted line is the ordinary least square regression slope (±S.E). See (*24*) for sources of taxon images.