



# A tiny fraction of all species forms most of nature: Rarity as a sticky state

Egbert H. van Nes<sup>a,1</sup> , Diego G. F. Pujoni<sup>b</sup>, Sudarshan A. Shetty<sup>c</sup>, Gerben Straatsma<sup>a</sup>, Willem M. de Vos<sup>c,d</sup> , and Marten Scheffer<sup>a,1,2</sup>

Contributed by Marten Scheffer; received December 23, 2022; accepted November 11, 2023; reviewed by Tadashi Fukami and Jonathan M. Levine

Using data from a wide range of natural communities including the human microbiome, plants, fish, mushrooms, rodents, beetles, and trees, we show that universally just a few percent of the species account for most of the biomass. This is in line with the classical observation that the vast bulk of biodiversity is very rare. Attempts to find traits allowing the tiny fraction of abundant species to escape rarity have remained unsuccessful. Here, we argue that this might be explained by the fact that hyper-dominance can emerge through stochastic processes. We demonstrate that in neutrally competing groups of species, rarity tends to become a trap if environmental fluctuations result in gains and losses proportional to abundances. This counter-intuitive phenomenon arises because absolute change tends to zero for very small abundances, causing rarity to become a “sticky state”, a pseudoattractor that can be revealed numerically in classical ball-in-cup landscapes. As a result, the vast majority of species spend most of their time in rarity leaving space for just a few others to dominate the neutral community. However, fates remain stochastic. Provided that there is some response diversity, roles occasionally shift as stochastic events or natural enemies bring an abundant species down allowing a rare species to rise to dominance. Microbial time series spanning thousands of generations support this prediction. Our results suggest that near-neutrality within niches may allow numerous rare species to persist in the wings of the dominant ones. Stand-ins may serve as insurance when former key species collapse.

biodiversity | competition | rarity | neutrality

Ecologists have long been puzzled by the enormous amount of rare species in nature (1–3). The numerous studies of this phenomenon have traditionally focused on the shape of species abundance distributions (4). However, different processes can generate similarly shaped distributions (5). Therefore, it remains difficult to draw mechanistic conclusions on the basis of the observed shape of a distribution. Also, the implications of shape by itself are difficult to grasp. A somewhat more intuitive angle of addressing the same phenomenon is asking how unequal abundances are, or—more specifically—how many species are needed to explain most of the mass in natural communities (6–8). The first results of such studies have attracted much attention as they revealed a situation of “hyperdominance” in which a tiny fraction of the species takes most of the biomass. For instance, analysis of the extensive data from the Amazon forest revealed hyperdominance (8) with as little as 1% of the thousands of tree species accounting for half the carbon storage (7). At the other end of the size spectrum, in bacteria (9) and lake plankton (10), competition between a multiplicity of asexually reproducing strains often dominates patterns of niche use, and a minor headstart has been shown to facilitate complete monopolization of habitats by a single clone (11). Here, we ask how common such hyperdominance is, and what—if anything—patterns may tell us about the question how many species we need for a functioning ecosystem. If a few percent of the species do indeed make up most of the biomass, what then is the secret of those species? Are rare species in some way inferior? And if so, when it comes to biodiversity preservation, is the vast majority of the species that is so rare, perhaps irrelevant for ecosystem functioning? To address those issues, we set out to take a fresh look at what is perhaps the oldest and most fundamental challenge in ecology: understanding what drives abundance and rarity of species.

## Material and Methods

**Data Compilation and Analysis.** We compiled a database with various communities based on the datasets compiled by Straatsma and Egli (12, 13). We complemented the data sets of mushrooms, fish, crustaceans, trees seedlings, rodents, winter annuals, summer annuals, ants, and birds, with phytoplankton data, bacteria, and Amazonian tree species (*SI Appendix, Table S1*). The data of bacteria were part of the Earth Microbiome Project (14) and were downloaded from Qiita (<http://qiita.microbio.me>, study ID's 945 and 550) (15). In all datasets,

## Significance

Data from the human microbiome as well as communities of flies, rodents, fish, trees, plankton, and fungi suggest that consistently a tiny fraction of the species accounts for most of the biomass. We suggest that this may be due to an overlooked phenomenon that we call “stickiness” of rarity. This can arise in groups of species that are equivalent in resource use but differ in their response to stochastic stressors such as weather extremes and disease outbreaks. Stickiness is not absolute though. In our simulations, as well as natural time series from microbial communities, rare species occasionally replace dominant ones that collapse, supporting the insurance theory of biodiversity. Rare species may play an important role as backups stabilizing ecosystem functioning.

Author contributions: E.H.v.N. and M.S. designed research; E.H.v.N. performed research; E.H.v.N., D.G.F.P., S.S., G.S., and W.M.d.V. analyzed data; and E.H.v.N. and M.S. wrote the paper.

Reviewers: T.F., Stanford University; and J.M.L., Princeton University.

Competing interest statement: In 2019, M.S. and J.M.L. were co-authors in a perspective paper.

Copyright © 2024 the Author(s). Published by PNAS. This article is distributed under [Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 \(CC BY-NC-ND\)](https://creativecommons.org/licenses/by-nc-nd/4.0/).

<sup>1</sup>E.H.v.N. and M.S. contributed equally to this work.

<sup>2</sup>To whom correspondence may be addressed. Email: [marten.scheffer@wur.nl](mailto:marten.scheffer@wur.nl).

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2221791120/-/DCSupplemental>.

Published January 2, 2024.

we sorted the species on the density of individuals and calculated the minimum fraction of the species that have 50% or more of the total number of individuals.

**Model.** To illustrate the effects of response diversity to environmental conditions and natural enemies on otherwise neutral coexistence, we use a simple model of random drift in abundance ( $N$ ) among a number of species ( $i$ ). Total carrying capacity of the environment ( $K$ ) is fixed; all species are identical in terms of competitive power (the competition coefficients of all species are 1). Diversity of responses of mortality and growth rates to a stochastic environment is represented by making each species subject to a unique time series of randomly drawn proportional gains or losses (a Wiener process  $dW$  with SD  $\sigma N_i$ ):

$$\frac{dN_i}{dt} = N_i \left( 1 - \frac{\sum N_j}{K} \right) + \sigma N_i \frac{dW}{dt}. \quad [1]$$

This stochastic differential equation was solved using an Euler-Maruyama scheme with a fixed time step ( $\Delta t = 0.01$ ), where we draw each time step the stochasticity from a normal distribution  $\mathbf{N}$ , with a mean of 0 and the SD of  $\sigma N_{i,t} \sqrt{\Delta t}$ :

$$N_{i,t+\Delta t} = N_{i,t} + N_{i,t} \left( 1 - \frac{\sum N_{j,t}}{K} \right) \Delta t + \mathbf{N}(0, \sigma N_{i,t} \sqrt{\Delta t}). \quad [2]$$

Note that we did not introduce a critical population density below which a species is considered extinct. Extending this model in *SI Appendix*, we studied the effect of such a threshold as well as varying carrying capacity, density-dependent mortality, additive noise, and correlated noise (details in *SI Appendix*, sections S5–S8).

**Stochastic Potential Landscapes.** To shed light on a potential underlying mechanism, we show that despite (time-averaged) neutrality, dominance and rarity can have the character of stochastic alternative attractors, which we will call “sticky states”, cf. ref. 16. We do that by using the stochastic model to generate potential landscapes. A potential landscape is an intuitive representation of the stability of a dynamical system. The slope of the potential landscape should be proportional to the rate of change of the dynamical system (17). The potential decreases along trajectories, and valleys represent basins of attraction. For systems with one state variable and additive Gaussian white noise, there is a one-to-one relation between the stationary probability density function and the potential (18). Our model is too complex to derive an exact potential function. Moreover the equilibria we studied are “pseudo-equilibria” and exist due to stochasticity (19). Therefore, we construct an approximate stochastic potential landscape for our model by applying the method of Livina et al. (18) to simulated data. To do this, we first determined the stationary probability density function by long simulations. We simulated 100 times 101,000 time units with random initial conditions. The first 1,000 steps were discarded, and from the other parts we saved each 100 time units one biomass value of one of the simulated species. We made a smoothed probability density function using a kernel smoother (Gaussian kernels with a standard bandwidth ( $bw$ ) depending on the SD and the number of data points ( $n$ ) (20):  $bw = 1.06 \text{ SD } n^{-1/5}$ ). We use a minus-log transformation (18) to approximate the potentials (Fig. 2 and *SI Appendix*, Fig. S5). The potentials in this approach have arbitrary units (21).

## Results and Discussion

**Prevalence of Hyperdominance across Communities.** We start our analysis by asking how widespread the phenomenon of hyperdominance is in nature? As a first step, we analyse abundance patterns in a wide range of natural communities including groups as diverse as the human intestinal bacteria, phytoplankton, trees, flies, fungi, rodents, and fish. Obviously, this collection is far from exhaustive. However, the results do suggest that quite universally a tiny fraction of the species accounts for the bulk of the total (Fig. 1). Especially in species-rich communities, a few percent of the species usually account for half of the counts. In fact, it is not uncommon that a single species takes half of the counts even if there are many species in the community (the sharply delineated

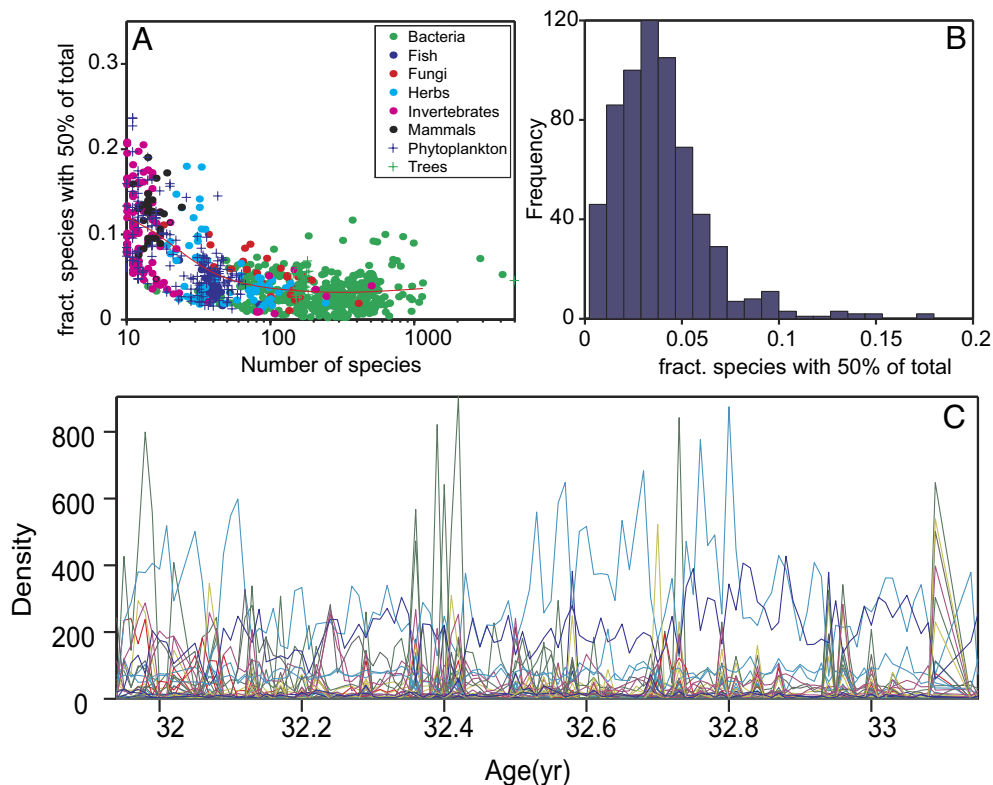
lower border of the cloud of points in Fig. 1A). For communities where few species are recorded, the fraction needed to account for half of the total rises, a pattern that may be explained as a statistical sampling effect (*SI Appendix*, section S2). An implication is that our dominance estimate is conservative. Very rare species will often be missed in censuses, implying an underestimate of the total number of species in communities and thus an overestimate of the fraction accounting for half of the total of individuals or biomass. For instance, if one species accounts for half of the biomass, in a community of 20 species that corresponds to 5%. However, if we missed 20 rare species in our census, the real fraction accounting for half of the biomass would be 2.5%.

While the fraction of species that accounts for half the counts may seem a rather arbitrary indicator, it has the advantage of being intuitive and is in fact well correlated to other well-known measures of inequality such as the Gini index (*SI Appendix*, section S3).

Most of our data refer to abundance. As abundance tends to vary strongly with body size, one might suspect size variation to explain part of the abundance patterns (23). However, variation in individual size is unlikely to be the main explanation for the ubiquitous occurrence of hyperdominance. For instance, in the extensive Amazon tree data, there is no clear relationship between abundance and typical size (8), although large trees do contribute more to total biomass (7). Also, our bacterial community data are based on metagenome analysis rather than individual counts, yet show surprisingly high levels of dominance as other communities we analysed. These patterns thus suggest that whatever community we look at, be it gut bacteria, fish, or Amazon trees, the vast bulk of the species is extremely rare, leaving just a few or even one single species to dominate. Framing it in another way: a beginning taxonomist needs to know only a few percent of the species (the most abundant ones) to recognize half of what they find in nature.

**Alternations of Dominance.** It is generally thought that common species tend to remain common over ecological timescales (24). However, judging longer-term persistence is difficult as time series covering sufficient numbers of generations are rare. A clear exception are microbial systems, which can be studied for thousands of generations. Such data do indeed provide ample evidence for long-term instability of dominance. For instance, recent work reveals that over time, different species can take dominant positions in the human microbiome (Fig. 1C). Similarly, in plankton communities, dominance by a single species is common but typically short-lived as other species take the dominant position leading to unpredictable alternations both under controlled laboratory conditions (25) (*SI Appendix*, section S4) and in natural communities (26). The idea that under the same environmental condition different species may rise to dominance is also in line with studies across large numbers of lakes, revealing that while the presence of a functional group is predictable, the identity of the dominant species is not (27).

The more than 10,000-fold longer generation times of trees make it difficult to reconstruct long-term intergenerational dynamics. However, detailed studies suggest that even in tropical forests, there are marked changes of relative species abundances over time (28–30). Functional redundancy and “near neutrality” may be characteristic features of such diverse communities as suggested for tropical forest (31), plankton (32), bacteria (33), beetles (34), and other taxonomic groups (35, 36). In conclusion, various lines of evidence suggest instability of dominance by functionally similar species over time. A dominant species now may thus not have been dominant in the past and may well be replaced by other species fulfilling a similar function in the future.



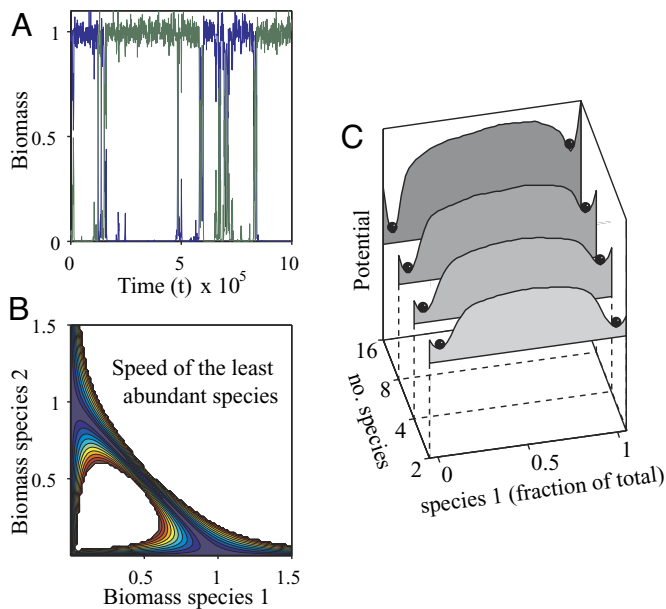
**Fig. 1.** Patterns of dominance across natural communities. (A) The fraction of species needed to account for 50% of the total individuals across communities as a function of the total number of species in the community. Each dot represents one community. (B) Frequency distribution (mean 0.039) across communities of the fraction accounting for 50% of the counts for communities with more than 20 species. (C) An example of fluctuations in dominance for a community of gut bacteria based on data from the male subject reported in ref. 22 (slightly smoothed using a Gaussian filter with a  $bw$  of 2/365 year; we excluded *Bacteroides* that was very dominant).

### Response Diversity with Neutral Competition as an Explanation.

The observation that a tiny fraction of the species dominate the biosphere, while such hyperdominant positions may occasionally be overtaken by previously rare species is puzzling. Could this hint at the way in which abundance and rarity are regulated across widely different communities including birds, trees, and gut bacteria? Thinking about potential explanations inevitably lead us back to a central but basically unresolved question in ecology: Does each species have a distinctive niche, or are many species functionally equivalent (31, 37–39)? The classical idea is that the unequal abundances of species reflect the size of the unique niche that they have been able to acquire over evolutionary history (40, 41). In this view, the explanation for the extraordinary dominance of some species is essentially their intrinsic superiority. A complementary view is that large groups of species may basically share a single niche and within this niche are close to neutral (equivalent) in competitive strength (31). Simple random walk-through demographic stochasticity may explain dominance in such neutral models of competition. However, such models fail to generate the pronounced fluctuations in population densities that are found in nature (29). This may be explained by the fact that this type of null models considers mortality and recruitment to be entirely random at the individual level. Such demographic stochasticity neglects the fact that, even if there is functional equivalence when it comes to resource use, species will tend to differ in their responses to various stressors. Such “response diversity” [sensu (42)] should cause the effect of environmental fluctuations and natural enemies to be more correlated for individuals within species than between species (29, 43, 44). Indeed, models with an interplay of environmental randomness with competition that is “symmetric” or “time-averaged

neutral” have been studied extensively, demonstrating that such an interplay of forces can generate realistically looking species abundance distributions (43, 45–47).

**Rarity as a Sticky State.** To explore a more mechanistically how an interplay between neutral competition and environmental fluctuations might cause the vast majority of species to be rare, we use a simple model (*Material and Methods*). To see the forces at play, we start with only two species (Fig. 2). The two species are entirely neutral competitors, implying that in the deterministic case ( $\sigma = 0$ ), simulations will end up with a neutrally stable mix in which their summed abundances match the carrying capacity (a point on their identical zero-growth isoclines). The eye-opener comes if we add the fluctuating environment ( $\sigma > 0$ ). Rather than generating a continuous distribution of states, this simple system ends up with one species being very rare most of the time (Fig. 2A). Since two species share one environment, rarity of one species implies that the other is close to carrying capacity. The key to understanding why the system dwells most of the time in either of the extreme states is that in the vicinity of these two alternative “winner-takes-all” situations, rates of change of the rarest species are very slow (Fig. 2B). As a result, the system will spend relatively more time in such slow places, and the stochastic potential landscape (19) computed from the probability density reveals alternative pseudo attractors (19). The system behaves as if there were two alternative stable states, even though both species are entirely equivalent. Expanding this to more species, the behavior remains qualitatively similar, except that only one species tends to be dominant at any time while the rest is rare. Thus, for each of the (equivalent) species, the chances of being dominant shrink and the well in the stochastical potential of



**Fig. 2.** Dynamical properties of a neutral competition model illustrating how dominance and rarity arise as alternative quasi attractors in a stochastic setting. (A) In a two-species situation one of the two dominates most of the time, punctuated by occasional stochastically induced transitions ( $\sigma = 0.04$ ). (B) Plotting the rate of change of the least abundant species (blue is slow, red is fast) reveals slowness around the two trivial equilibria [(1,0) and (0,1)]. As a result, the frequency distributions of any species are bimodal and the stochastic potential landscape suggests two alternative attractors (panel C front panel). As the number of species increases the attraction basin representing the resilience of the rare state of any of the (equivalent) species grows at the expense of that of the abundant state (panel C).

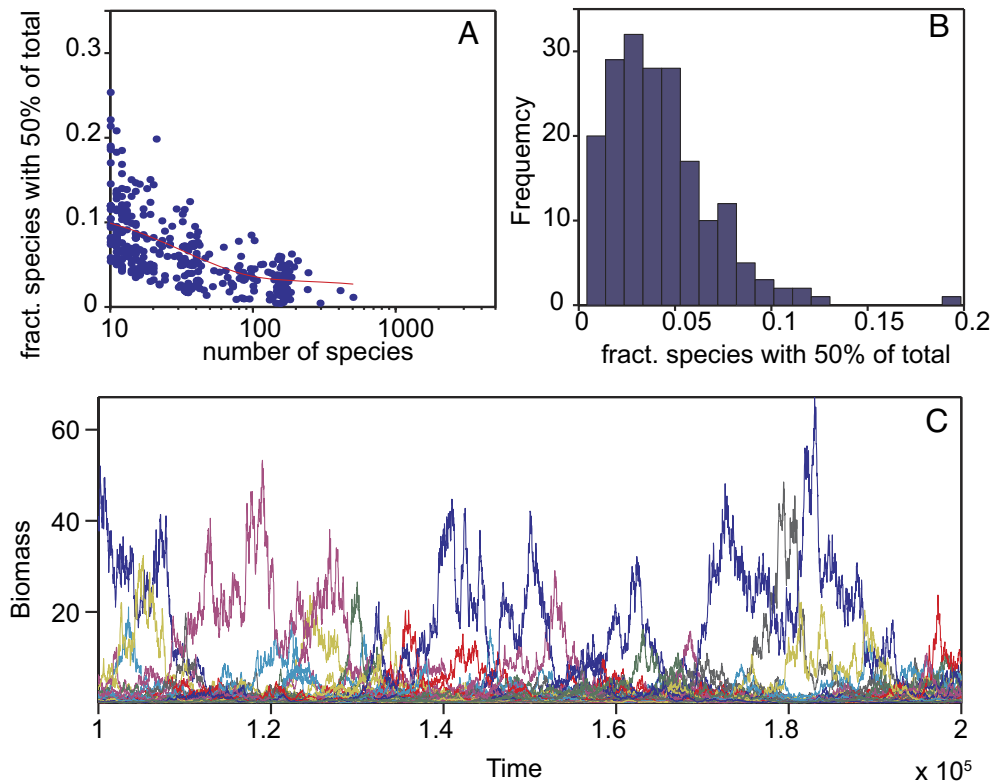
the rare state becomes wider and relatively deeper (Fig. 2C). These simulations suggest an intuitive interpretation for the long-standing question of why most species are so rare. Loosely framed, our results suggest that most species might be rare most of the time simply because rarity tends to be a sticky state. For loose analogy, think of a thousand ants crawling over a floor randomly. If there is a stickier spot on the floor where their movement is slowed down, more ants eventually become concentrated there (see simulation in [Movie S1](#)). The spot is not a “Hotel California”: Ants can leave, but spend more time in the sticky zone.

Simulations with larger communities illustrate how the same process can generate patterns of inequality (Fig. 3 A and B) that closely mimic nature (Fig. 1 A and B). Much as in the time series of real communities (Fig. 1C), the simulated species take turns in dominating (Fig. 3C). As discussed later, patterns in nature will of course be coshaped by a range of mechanisms that we do not account for in our minimal model. Nonetheless, as illustrated by our simulations (Fig. 3), tuning just the variance of the random gains and losses,  $\sigma$ , natural patterns of hyperdominance can already be mimicked closely. This outcome is unlikely to be an artefact of the particular model formulation we explored as similar may be produced from a diverse range of models that combine stochasticity with (time-averaged) neutral competition (43, 45–49). On a more abstract level, such results are also in line with the general notion that multiplicative random shocks (i.e., the noise factor is a multiplier of population density  $N$ ) tend to produce log-normal distributions (50, 51) ([SI Appendix, section S2](#)). As we illustrated, a more mechanistic way of understanding such patterns might be to think of the “stickiness” of rarity. The cause of this stickiness is analogous to the counterintuitive dynamics of exponential growth. Even if relative rates of change are the same as those of abundant species, the absolute rates of change of rare species will always be very low, causing a tendency for this state to linger on.

**Robustness of Model Results.** In many ways, our minimalistic model represents a somewhat pathological limit case. For instance, we do not consider exchange with populations elsewhere, we have no threshold below which populations go extinct, we assume perfect neutrality, the perturbation regimes of the different species are entirely uncorrelated, and the perturbation regime works in a multiplicative way, causing absolute change to be proportional to population size. In [SI Appendix, sections S5–S9](#), we systematically analyze robustness of the sticky state phenomenon and the resulting pseudo attractors to those assumptions as well as the effects of chaos and different levels of environmental fluctuation. Here is a summary of what we find.

The complexity of embedding populations in a larger world, with exchange between populations of the same species elsewhere is challenging to represent realistically. If one is interested in how spatial embedding may affect dynamics of populations at very low densities, one simple way to capture that effect is to assume a small influx from elsewhere (52). The idea is that populations in nature are embedded in networks of somewhat asynchronously fluctuating communities in a heterogeneous world. Immigration from the larger metacommunity will statistically promote abundance of the locally rarest species most. This is analogous to the “storage effect” where populations have a differential response to environmental fluctuations and are prevented to go extinct by recruitment from a seed bank or other “safe haven” unaffected by the local environmental ups-and-downs (53, 54). The effect on the dynamics can be mimicked by adding a small immigration term to each species (52). Such a trickle reduces the “sticky” nature of extreme rarity. This smooths the overall pattern, promoting more frequent alternations in dominance and increasing the fraction of species that have a substantial abundance ([SI Appendix, section S5.1](#)). Analogous effects of reduced stickiness occur in our chaos-driven models and in classical predator–prey cycles, which in the absence of the stabilizing effect of spatial heterogeneity tend to become very long as the species pass through long periods of near-extinction (52). To explore the interactive effect of connected populations (rather than a one-way influx from an independent outer world), we also explored the effect of spatial exchange between communities replicated in connected spatial units ([SI Appendix, section S8](#)). Pronounced hyperdominance with occasional alternations remains, but depending on the level of connectivity (through a diffusive exchange rate) patterns easily become synchronized between the spatial units. Thus, in a spatial world, the contrast between dominance and rarity may be ameliorated, while dominance tends to be contagious. The latter would be consistent with abundance patterns being similar over larger regions.

Next, we analyzed whether stickiness can remain intact if we add a threshold below which a population goes extinct (rather than allowing extremely small densities). Not surprisingly, adding such a cut-off critical population level causes all species to go extinct at time infinity ([SI Appendix, Fig. S12](#)). More precisely, all species except one. That is because extinction in our neutral communities happens to the rare species, and eventually, the remaining single species is practically risk-free because it is usually never driven into the sticky state except when the noise levels are very high. For cut-off levels of  $\sim 10^{-5}$  of the carrying capacity, the median time before a species goes extinct tends to be in the order of 10,000 generations. Thus, extinction in those simulations is a very slow process. Two mechanisms may prevent species numbers from dwindling: 1) occasional addition of new species through speciation or the arrival of new species from elsewhere and 2) an influx of individuals to each species causing a rescue effect. Such mechanisms have been explored extensively previously (55, 56). In the tradition of the neutral theory of biodiversity (31), speciation is seen as the main counterforce, whereas arrival of new species



**Fig. 3.** Simulations with larger communities illustrate how neutral competition with response diversity can generate patterns of inequality that closely mimic nature (cf. Fig. 1). (A) The fraction of species needed to account for 50% of the total individuals across simulated communities as a function of the total number of species in the community. Each dot represents one community. (B) Frequency distribution (mean 0.043) across communities of the fraction accounting for 50% of the counts for communities with more than 20 species. (C) Example of a model run with 100 species and a sigma 0.005.

is at the roots of the classical theory of island biogeography (57). By contrast in metapopulation theory, the rescue effect is emphasized (55). We simulated such counterforces (influx of species or individuals) to explore whether in the presence of an extinction threshold, the sticky-state effect can be robust, while still preventing dwindling numbers of species. The occasional arrival of a new species (either through speciation or through immigration) is the simplest mechanism. This does not have the effect of preventing population densities to become very small (as does the rescue effect). It therefore leaves the stickiness effect unaffected, while compensating for the extinction rate in our simulations depends on the speciation/colonization rate and the extinction threshold (*SI Appendix, Fig. S16*). As we saw, in the absence of any rescue effect, species in our simulations go extinct in about 10,000 generations while speciation in isolated populations happens in about 10 to 100 generations (58). Thus speciation or arrival of new species may plausibly prevent locally dwindling numbers of species, while it does not prevent stickiness effects. This is different for a fixed influx of individuals, as this can destroy the stickiness if it becomes too strong (*SI Appendix, Fig. S13*). However, simulations show that in the presence of an extinction threshold the sticky phenomenon remains robust over several orders of variation in the magnitude of the influx (depending on the extinction threshold, *SI Appendix, Fig. S13*). Thus, the rescue effect may prevent extinction without destroying the stickiness effect. We also simulated spatial dynamics explicitly, by running our model with extinction threshold in a set of connected patches, with diffusive exchange between them. Not surprisingly, the results show that such a spatial setting makes extinction much less likely (*SI Appendix, Fig. S14*), especially if there are larger numbers of patches involved (*SI Appendix, Fig. S15*). In conclusion, adding

a threshold for extinction to our model leads to loss of species, it is an extremely slow process that is slowed down even further influx of individuals in spatial settings without affecting the stickiness effect. The resulting extremely slow rates of extinctions may be easily overwhelmed by speciation.

We also checked robustness against the neutrality assumption (*SI Appendix, section S5.2*). If we give one species a slight competitive advantage, the balance between the two pseudo attractors is easily lost, suggesting that it might be a fragile result. Nonetheless, if we further increase realism by accounting for the fact that abundant species tend to attract more natural enemies (adding nonlinear density-dependent mortality), the alternative attractors return and are even more resilient than in the case of neutral competition. Arguably, such nonlinear effects of natural enemies do indeed tend to stabilize near-neutral coexistence in nature (37, 59, 60).

As with the temporal storage effect, the assumption that species respond differently to environmental fluctuations is crucial for the results (*SI Appendix, section S5.3*). If the stochastic fluctuations are synchronous for all species, the model becomes fully neutral and the stickiness disappears (*SI Appendix, Fig. S7*). It can be easily understood from the two-species model that in the limit-case when perturbations affect species proportionally and identically, relative abundances will never change, so no dominance can emerge. Simulations perturbation regimes that are partially correlated between species illustrate that patterns are robust as long as we assume some level of response diversity. Another crucial assumption is the multiplicative nature of the effects of perturbations (*SI Appendix, section S5.4 and Fig. S8*). If both species experience perturbations that are independent of the state (additive noise instead of multiplicative noise), there is no sticky state, and dominance shifts rapidly. This shows that the phenomenon of quasiattractors is really caused

by the fact that at low densities, proportionality causes absolute rates of change to become very slow.

It is also important to note that fluctuations in environmental conditions are not the only drivers of population fluctuations in nature. Evolution may drive (or prevent) critical transitions (61), and intrinsic cycles and chaos resulting from nonlinear species interactions can be a major driver of population fluctuations (25, 62). Outbreaks of diseases or other natural enemies are notorious examples. Given enough generations to pass such dynamics may in involve coevolutionary arms races as hypothesized for bacteria and their phage enemies (63–66). Adding dynamic natural enemies to the deterministic version of the neutral model easily leads to chaotic dynamics, causing patterns of hyperdominance that are very similar to the inequality produced by the stochastically forced model (*SI Appendix, section S6 and Fig. S9*). In nature, the effects of environmental fluctuations and intrinsic chaos will typically be intertwined (67), and not surprisingly, simulating such a mix produces similar patterns (*SI Appendix, section S6*).

In conclusion, relaxing the assumptions of the model in various ways tends to leave the overall predictions intact, suggesting that the sticky state prediction may not hinge on an overly simplistic limit case. Nonetheless, our exploratory analyses suggest that spatial complexity or high environmental stochasticity may blur the patterns of dominance we found (*SI Appendix, sections S5–S8*). The same is true for two mechanisms that we did not address explicitly. First, natural enemies tend to take a higher toll on the more abundant species which should ultimately reduce dominance and promote diversity (59, 60). Second, niche differentiation remains a major driver of abundance patterns. Neutral competition is to be expected only within functionally similar species that essentially share a single niche (37). This implies that larger communities may be seen as consisting of smaller neutral communities for each niche. Hyperdominance will be reduced by such a niche structure, simply because the winner-takes-all dynamics are limited to the smaller subsets.

**Implications.** Our explorative analysis of abundance data confirms a classical enigmatic observation: Most species are exceedingly rare. As illustrated by the diverse set of data we explored, a few percent of the species is responsible for most of what we see in nature, be it in mushrooms, trees, beetles or bacteria. Demonstrating why this is so, remains challenging. However, in line with earlier theoretical analyses, we illustrate that the observation is consistent with the view that nature is populated by large groups of functionally equivalent species that compete neutrally for resources but nonetheless differ in their sensitivity to natural enemies and environmental fluctuations. One implication from such theoretical findings is that dominance does not have to result from superiority in competition for resources. It may seem natural that striking dominance of particular species should be explainable from their specific traits. However, it has turned out surprisingly difficult to identify such explanations for success (7, 8, 24). While particular species may well be wired for success, our analysis and other models of stochastic time-averaged neutrality (43, 45–49) suggest that hyperdominance can emerge

even in the absence of inherent superiority. What we see dominating nature today might thus well be an “accidental elite,” even if, admittedly, this will remain hard to prove in practice.

Perhaps more importantly, the mechanisms we explored in our model help reconcile the influential neutral theory of biodiversity (31, 68) to the notion that the countless rare species in nature cannot be considered redundant, but instead serve as an insurance to maintain function in times of adverse events (69, 70). Even if rare species perform the same function as their more abundant counterparts, their different sensitivity to stressors and natural enemies, or symbiotic relations enables a stable performance of communities in the face of fluctuating conditions and pathogen outbreaks. A range of empirical studies does confirm that more diverse communities tend to have a more stable performance under fluctuating conditions (71–73). A fascinating proof of principle for the interplay of functional redundancy and response diversity comes from experimental work on bacteriophage outbreaks in cheese-making cultures (33, 66). In simple constructed communities that contain all necessary functional groups as single strains, such outbreaks are devastating for functionality. By contrast in the diverse communities that are propagated by generations of cheese makers, such crashes do not affect overall activity as functionally equivalent strains compensate for such losses. It may well be that the dominance alternations we see in the human microbiome (Fig. 1C) are in part driven by similar chaotic interference with phages that are abundantly present (74). However, we are far from being able to test the role of functional redundancy and response diversity in the multitude of ecological communities that form the web of life on which humanity ultimately depends. Nonetheless, while our results suggest that nature is dominated by a tiny fraction of the species, they are consistent with the view that the remaining vast majority is important for stabilizing long-term ecosystem functioning.

**Data, Materials, and Software Availability.** Previously published data were used for this work (each source is cited in the manuscript).

**ACKNOWLEDGMENTS.** We are grateful for the availability of extensive data collected in a series of diverse and usually laborious field studies (see *SI Appendix* for a full set of references). In particular, we wish to thank Frank Roozen and Gerben van Geest for data on plankton, Thomas Olszewski for sharing the data on Permian brachiopod communities, and Simon Egli for the mushroom data. Part of the tree community data come from the BCI forest dynamics research project founded by S. P. Hubbell and R. B. Foster and now managed by R. Condit, S. Lao, and R. Perez under the Center for Tropical Forest Science and the Smithsonian Tropical Research in Panama. Numerous organizations have provided funding, principally the US NSF, and hundreds of field workers have contributed.

Author affiliations: <sup>a</sup>Aquatic Ecology and Water Quality Management Group, Environmental Science Department, Wageningen University, Wageningen NL-6700 AA, The Netherlands; <sup>b</sup>Federal University of Minas Gerais, Departamento de Biologia Geral, Instituto de Ciências Biológicas, Laboratório de Limnologia, Ecotoxicologia e Ecologia Aquática, Belo Horizonte MG CEP 31270-901, Brazil; <sup>c</sup>Laboratory of Microbiology, Wageningen University, Wageningen NL-6700 EH, The Netherlands; and <sup>d</sup>Human Microbiome Research Program, Faculty of Medicine, University of Helsinki, Helsinki 00014, Finland

1. G. E. Hutchinson, Homage to Santa-Rosalía or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159 (1959).
2. K. J. Gaston, *Rarity* (Chapman & Hall, London, 1994), p. 205.
3. F. W. Preston, The commonness, and rarity, of species. *Ecology* **29**, 254–283 (1948).
4. B. J. McGill *et al.*, Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.* **10**, 995–1015 (2007).
5. R. A. Chisholm, S. W. Pacala, Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 15821–15825 (2010).
6. T. Fung, L. Villain, R. A. Chisholm, Analytical formulae for computing dominance from species-abundance distributions. *J. Theor. Biol.* **386**, 147–158 (2015).
7. S. Fauset *et al.*, Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.* **6**, 6857 (2015).
8. H. Ter Steege *et al.*, Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092 (2013).
9. S. S. Li *et al.*, Durable coexistence of donor and recipient strains after fecal microbiota transplantation. *Science* **352**, 586–589 (2016).
10. L. De Meester, A. Gomez, B. Okamura, K. Schwenk, The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecolog. Intern. J. Ecol.* **23**, 121–135 (2002).
11. L. De Meester, A. Gómez, B. Okamura, K. Schwenk, The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecolog.* **23**, 121–135 (2002).
12. G. Straatsma, S. Egli, Rarity in large data sets: Singletons, modal values and the location of the species abundance distribution. *Basic Appl. Ecol.* **13**, 380–389 (2012).
13. G. Straatsma, S. Egli, Rarity in large data sets: Singletons, modal values and the location of the species abundance distribution. Supplementary data. <https://ars.els-cdn.com/content/image/1-s2.0-S1439179112000333-mm2.zip>. Accessed 29 January 2018.
14. L. R. Thompson *et al.*, A communal catalogue reveals Earth's multiscale microbial diversity. *Nature* **551**, 457–463 (2017).

15. A. Gonzalez *et al.*, study ID's 945 and 550. Qiita: rapid, web-enabled microbiome meta-analysis. *Nature Methods* **15**, 796–798 (2018).
16. N. Bou-Rabee, M. C. Holmes-Cerfon, Sticky brownian motion and its numerical solution. *SIAM Rev.* **62**, 164–195 (2020).
17. S. H. Strogatz, *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry and Engineering* (Addison-Wesley Publishing Company, 1994), pp. 1–498, Reading.
18. V. N. Livina, F. Kwasiński, T. M. Lenton, Potential analysis reveals changing number of climate states during the last 60 kyr. *Climate of the Past* **6**, 77–82 (2010).
19. W. Horsthemke, R. Lefever, *Noise-Induced Transitions: Theory and Applications in Physics, Chemistry, and Biology* (Springer-Verlag, Berlin, 1984), p. 318.
20. B. W. Silverman, *Density Estimation for Statistics and Data Analysis* (CRC Press, New York, 1986), p. 176.
21. M. Hirota, M. Holmgren, E. H. Van Nes, M. Scheffer, Global resilience of tropical forest and savanna to critical transitions. *Science* **334**, 232–235 (2011).
22. J. G. Caporaso *et al.*, Moving pictures of the human microbiome. *Genome Biol.* **12**, 1 (2011).
23. H. Morlon *et al.*, Taking species abundance distributions beyond individuals. *Ecol. Lett.* **12**, 488–501 (2009).
24. K. J. Gaston, Common ecology. *BioScience* **61**, 354–362 (2011).
25. E. Benincà *et al.*, Chaos in a long-term experiment with a plankton community. *Nature* **451**, 823–826 (2008).
26. C. S. Reynolds, *The Ecology of Phytoplankton* (Cambridge University Press, 2006).
27. C. Kruk *et al.*, Phytoplankton community composition can be predicted best in terms of morphological groups. *Limnol. Oceanogr.* **56**, 110–118 (2011).
28. K. J. Feeley, S. J. Davies, R. Perez, S. P. Hubbell, R. B. Foster, Directional changes in the species composition of a tropical forest. *Ecology* **92**, 871–882 (2011).
29. M. Kalyuzhny *et al.*, Temporal fluctuation scaling in populations and communities. *Ecology* **95**, 1701–1709 (2014).
30. M. Katabuchi *et al.*, *Contrasting Outcomes of Species- and Community-Level Analyses of the Temporal Consistency of Functional Composition* (Wiley Online Library, 2017).
31. S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton University Press, Princeton, 2001), p. 375.
32. A. M. Segura *et al.*, Emergent neutrality drives phytoplankton species coexistence. *Proc. R. Soc. B* **278**, 2355–2361 (2011).
33. O. Erkus *et al.*, Multifactorial diversity sustains microbial community stability. *ISME J.* **7**, 2126–2136 (2013).
34. M. Scheffer *et al.*, The evolution of functionally redundant species; evidence from beetles. *PLoS One* **10**, e0137974 (2015).
35. R. Vergnon, E. H. Van Nes, M. Scheffer, Emergent neutrality leads to multimodal species abundance distributions. *Nat. Commun.* **3**, 663 (2012).
36. R. Vergnon, N. K. Dulvy, R. P. Freckleton, Niches versus neutrality: Uncovering the drivers of diversity in a species-rich community. *Ecol. Lett.* **12**, 1079–1090 (2009).
37. M. Scheffer, E. H. Van Nes, Self-organized similarity, the evolutionary emergence of groups of similar species. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 6230–6235 (2006).
38. M. Scheffer, E. H. Van Nes, R. Vergnon, Toward a unifying theory of biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 639–641 (2018).
39. J. M. Levine, J. HilleRisLambers, The importance of niches for the maintenance of species diversity. *Nature* **461**, 254–257 (2009).
40. R. H. MacArthur, R. Levins, Limiting similarity, convergence and divergence of coexisting species. *Am. Nat.* **101**, 377–385 (1967).
41. R. H. MacArthur, On the relative abundance of bird species. *Proc. Natl. Acad. Sci. U.S.A.* **43**, 293–295 (1957).
42. T. Elmqvist *et al.*, Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* **1**, 488–494 (2003).
43. M. Kalyuzhny, R. Kadmon, N. M. Shnerb, A neutral theory with environmental stochasticity explains static and dynamic properties of ecological communities. *Ecol. Lett.* **18**, 572–580 (2015).
44. D. Alonso, R. S. Etienne, A. J. McKane, Response to Benedetti-Cecchi: Neutrality and environmental fluctuations. *Trends Ecol. Evol.* **22**, 232 (2007).
45. M. Danino, N. M. Shnerb, Theory of time-averaged neutral dynamics with environmental stochasticity. *Phys. Rev. E* **97**, 042406 (2018).
46. J. S. Clark, Beyond neutral science. *Trends Ecol. Evol.* **24**, 8–15 (2009).
47. D. Kessler, S. Suweis, M. Formentin, N. M. Shnerb, Neutral dynamics with environmental noise: Age-size statistics and species lifetimes. *Phys. Rev. E* **92**, 022722 (2015).
48. J. Chave, Neutral theory and community ecology. *Ecol. Lett.* **7**, 241–253 (2004).
49. B. J. McGill, B. A. Maurer, M. D. Weiser, Empirical evaluation of neutral theory. *Ecology* **87**, 1411–1423 (2006).
50. S. Engen, B. E. Saether, Stochastic population models: Some concepts, definitions and results. *Oikos* **83**, 345–352 (1998).
51. R. M. May, "Patterns of species abundance and diversity" in *Ecology and Evolution of Communities*, M. L. Cody, J. M. Diamond, Eds. (Harvard University Press, Cambridge, MA, 1975), pp. 81–120.
52. M. Scheffer, R. J. De Boer, Implications of spatial heterogeneity for the paradox of enrichment. *Ecology* **76**, 2270–2277 (1995).
53. P. Chesson, Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–366 (2000).
54. P. Chesson, Multispecies competition in variable environments. *Theor. Popul. Biol.* **45**, 227–276 (1994).
55. I. Hanski, Single-species metapopulation dynamics: Concepts, models and observations. *Biol. J. Linn. Soc.* **42**, 17–38 (1991).
56. R. G. Gillespie, G. K. Roderick, Arthropods on Islands: Colonization, speciation, and conservation. *Annu. Rev. Entomol.* **47**, 595–632 (2002).
57. R. H. MacArthur, E. O. Wilson, *The Theory of Island Biogeography* (Princeton University Press, Princeton, 1967), p. 203.
58. A. P. Hendry, P. Nosil, L. H. Rieseberg, The speed of ecological speciation. *Funct. Ecol.* **21**, 455 (2007).
59. S. A. Schnitzer *et al.*, Soil microbes drive the classic plant diversity-productivity pattern. *Ecology* **92**, 296–303 (2011).
60. J. W. Terborgh, Toward a trophic theory of species diversity. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 11415–11422 (2015).
61. V. Dakos *et al.*, Ecosystem tipping points in an evolving world. *Nat. Ecol. Evol.* **3**, 355–362 (2019).
62. J. Huisman, F. J. Weissing, Oscillations and chaos generated by competition for interactively essential resources. *Ecol. Res.* **17**, 175–181 (2002).
63. M. G. Weinbauer, F. Rassoulzadegan, Are viruses driving microbial diversification and diversity? *Environ. Microbiol.* **6**, 1–11 (2004).
64. C. Winter, T. Bouvier, M. G. Weinbauer, T. F. Thingstad, Trade-offs between competition and defense specialists among unicellular planktonic organisms: The "killing the winner" hypothesis revisited. *Microbiol. Mol. Biol. Rev.* **74**, 42–57 (2010).
65. C. Xue, N. Goldenfeld, Coevolution maintains diversity in the stochastic "Kill the Winner" model. *Phys. Rev. Lett.* **119**, 268101 (2017).
66. E. J. Smid *et al.*, Functional implications of the microbial community structure of undefined mesophilic starter cultures. *Microb. Cell Fact.* **13**, S2 (2014).
67. O. N. Bjornstad, B. T. Grenfell, Noisy clockwork: Time series analysis of population fluctuations in animals. *Science* **293**, 638–643 (2001).
68. D. Alonso, R. S. Etienne, A. J. McKane, The merits of neutral theory. *Trends Ecol. Evol.* **21**, 451–457 (2006).
69. S. Yachi, M. Loreau, Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc. Natl. Acad. Sci. U.S.A.* **96**, 1463–1468 (1999).
70. M. Loreau, Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos* **91**, 3–17 (2000).
71. M. Loreau, C. Mazancourt, Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecol. Lett.* **16**, 106–115 (2013).
72. K. Gross *et al.*, Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments. *Am. Nat.* **183**, 1–12 (2014).
73. Y. Hautier *et al.*, Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* **348**, 336–340 (2015).
74. P. Manrique *et al.*, Healthy human gut phageome. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 10400–10405 (2016).