

Recent Advances and Issues in

# Environmental Science



**William Hunter, III**  
Editor

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**ENVIRONMENTAL SCIENCE**

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**ENVIRONMENTAL SCIENCE**

*Edited By*

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## Preface

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The field of environmental science is relatively new, but its importance cannot be overestimated. As with many scientific fields, the work of environmental science draws attention on many other sciences to solve problems that we face today. Due to its very broad and cross-disciplinary nature, there is not a consensus as to its correct definition. However, the definition for an environmental science program of study provided by the National Center for Education Statistics (part of the United States Department of Education) encapsulates this diverse field well: “A program that focuses on the application of biological, chemical, and physical principles to the study of the physical environment and the solution of environmental problems, including subjects such as abating or controlling environmental pollution and degradation; the interaction between human society and the natural environment; and natural resources management. Includes instruction in biology, chemistry, physics, geosciences, climatology, statistics, and mathematical modeling.”

As seen in the above description, environmental science is truly interdisciplinary, fostering wide-ranging relationships across sciences and math. However, the value of a solid, diverse, liberal-arts background to start, with emphasis in the social sciences, is also important. Communication of results with the general public, lawmakers, and other stakeholders and the creation of government policy will be critical. Therefore, understanding the functioning of government at the local, state, national, and global level will be important in helping to create policies that effectively deal with specific environmental issues.

Environmental science seeks answers to some of our biggest environmental challenges. Many of these tie into a greater concept of using the earth’s resources sustainably. For example, reducing greenhouse emissions that lead to global warming can be accomplished in a number of ways, such as developing more efficient cars and industrial processes while also developing renewable energy. Actively saving rainforest and other wild areas can also be invaluable in reducing greenhouse gases, as they will sequester large amounts of carbon while also preserving biodiversity. Looking at interactions such as these and producing models of their effects is all in the purview of environmental scientists.

A broad background in many sciences makes an effective environmental scientist and would include course work in ecology, biology, geology, statistics, and planning. The career field is equally broad and would include work in local municipalities (such as sewage treatment plant operators) and consulting with national governments in a specialty area such as geophysics. Employment can be found with local, state, and federal governments, private companies, colleges and universities, and lobbying groups.

The relevance of environmental science is visible all around us every day. Often the world news media is focused on large-scale environmental problems such as global warming. However, if you think about everyday local life at your community level, it does not take long to develop a list of questions relevant to environmental science.

How does your community get fresh drinking water? Where does your community dispose of solid waste? What level of treatment does community sewage receive before being discharged into natural waterways? Is your community welcoming to alternative forms of transit such as buses, bicycles, and pedestrians, or is it totally reliant on automobiles? Is your food grown in the local community or shipped from distant areas? Is your home safe from toxins and contaminants? Although seemingly cliché now, the saying “Think Global, Act Local” really can have large-scale beneficial results, and directly seeing local environmental issues makes them more tangible.

Due to its relevance on the local and global level and its diverse number of careers, the future of environmental science is strong. Employment will be found at a wide range of levels and for people with highly variable skills. The top levels of this field will need people with the ability to integrate wide-ranging data sets and understand their relevance, and those who have strong communication skills to translate these results to the general public. All of the science and resources that we can bring to bear on an environmental problem will mean nothing in the end if we cannot get people to act.

— **William Hunter III**

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## List of Abbreviations

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AChE	Acetylcholinesterase
AOGCMs	Atmosphere-ocean general circulation models
ARP	Acid regeneration plant
AUC	Area under the curve
BoliviaWET	Bolivia water evaluation trial
CCEs	Carboxy/cholinesterases
CCS	Carbon capture and storage
CDPH	California Department of Public Health
CI <sub>s</sub>	Confidence intervals
CMIP	Coupled Model Intercomparison Project
CNS	Central nervous system
COD	Chemical oxygen demand
CSC	China Steel Corporation
DE	Design effect
DEM	Digital elevation model
dxs	D-1-Eoxyxylulose 5-phosphate synthase gene
ECOD	7-Ethoxycoumarin-O-deethylase
EIA	Energy Information Administration
EIP	Extrinsic incubation period
EIS	Environmental impact studies
EKA	Environmental knowledge accumulation
EKC	Environmental knowledge creation
EKCP	Environmental knowledge circulation process
EKI	Environmental knowledge internalization
EKM	Environmental knowledge management
EKS	Environmental knowledge sharing
EKU	Environmental knowledge utilization
EM	Environmental management
EMF	Electromagnetic field
EMIS	Environmental management information system
EMS	Environmental management systems
ENM	Ecological niche modeling
EPD	Environmental Protection Department
EPI	Expanded program for immunization
ESRI	Environmental Systems Research Institute

FBR	Feeding buzz ratio
FPIC	Free, prior, and informed consent
GEEs	Generalized estimating equations
GIS	Geographic information system
GLMMs	Generalized linear mixed models
GSCM	Green supply chain management
GSTs	Glutathione S-transferases
HNT	Hubbell's 2001 neutral theory
ICC	Intracluster correlation coefficient
ICDDR, B	International Centre for Diarrheal Disease Research, Bangladesh
IPCC	Intergovernmental Panel on Climate Change
IQR	Interquartile range
IR	Incidence rate
ITT	Ishpingo–Tiputini–Tambococha
KC	Knowledge creation
KCP	Knowledge circulation process
kdr	Knock down resistance
KM	Knowledge management
MCE	Mediterranean climate extent
MOHFW	Ministry of Health and Family Welfare
MSP	Major surface protein
MSWI	Municipal solid waste incinerator
NAC	National Advisory Committee
NDVI	Normalized Difference Vegetation Index
NGO	Nongovernmental organization
NHL	Non-Hodgkin lymphoma
NREL	National Renewable Energy Laboratories
NSW	New South Wales
OR	Odds ratio
ORS	Oral rehydration salt
ORT	Oral rehydration therapies
PCA	Principal components analysis
PCDD/F	Polychlorinated dibenzo-p-dioxins and dibenzofurans
PCI	Project Concern International
PCI	Pulverized coal injection
PCR	Polymerase chain reaction
PDCA	Plan-do-check-action
PET	Polyethyleneteraphthalate
PNLTs	Pirbright-Miniature light-suction traps

PR	Prevalence ratio
RF	Radio frequency
RR	Relative rate
RRs	Rate ratios
SADs	Species-abundance distributions
SARs	Species-area relationships
SD	Severe diarrhea
SDS	Sodium dodecyl sulfate
SEA	Strategic Environmental Assessment
SIRs	Standardized cancer ratios
SODIS	Solar drinking water disinfection
SSs	Suspended solids
TCDD	2,3,7,8-Tetrachlorodibenzo-p-dioxin
TTC	Thermotolerant coliforms
TW	Terawatt
US EPA	United States Environmental Protection Agency
UV	Ultraviolet
WCRP	World Climate Research Programme
WHO	World Health Organization



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# Chapter 1

## Ecological Equivalence: Niche Theory as a Testable Alternative to Neutral Theory

C. Patrick Doncaster

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### INTRODUCTION

Hubbell's 2001 neutral theory (HNT) unifies biodiversity and biogeography by modeling steady-state distributions of species richness and abundances across spatio-temporal scales. Accurate predictions have issued from its core premise that all species have identical vital rates. Yet no ecologist believes that species are identical in reality. Here I explain this paradox in terms of the ecological equivalence that species must achieve at their co-existence equilibrium, defined by zero net fitness for all regardless of intrinsic differences between them. I show that the distinction of realized from intrinsic vital rates is crucial to evaluating community resilience.

An analysis of competitive interactions reveals how zero-sum patterns of abundance emerge for species with contrasting life-history traits as for identical species. I develop a stochastic model to simulate community assembly from a random drift of invasions sustaining the dynamics of recruitment following deaths and extinctions. Species are allocated identical intrinsic vital rates for neutral dynamics, or random intrinsic vital rates and competitive abilities for niche dynamics either on a continuous scale or between dominant-fugitive extremes. Resulting communities have steady-state distributions of the same type for more or less extremely differentiated species as for identical species. All produce negatively skewed log-normal distributions of species abundance, zero-sum relationships of total abundance to area, and Arrhenius relationships of species to area. Intrinsically identical species nevertheless support fewer total individuals, because their densities impact as strongly on each other as on themselves. Truly neutral communities have measurably lower abundance/area and higher species/abundance ratios.

Neutral scenarios can be parameterized as null hypotheses for testing competitive release, which is a sure signal of niche dynamics. Ignoring the true strength of interactions between and within species risks a substantial misrepresentation of community resilience to habitat loss.

The HNT unifies the disciplines of biodiversity and biogeography by modeling steady-state distributions of species richness and relative species abundance across spatio-temporal scales [1]. Surprisingly accurate predictions have issued from its core premise that all species are exactly identical in their vital rates. As a null hypothesis to explain what should be observed if all species were perfectly equal with respect to all ecologically relevant properties, it has proved hard to refute [2]. Yet no ecologist, including Hubbell, believes that species are equivalent in reality [3, 4]. The challenge

presented by HNT is to justify invoking anything more complex than ecological drift to define community structure [5]. Its extravagant simplicity has had an explosive impact on ecology (>1,100 citations, rising exponentially), because it appears to discount 100 years of traditional conventions on niche differentiation. If biodiversity encompasses the great richness of differently attributed species that constitutes the natural world, how can ecological equivalence yield such predictive power about the numbers of species [6]? If HNT is based on a ludicrous assumption [7], then our conceptual understanding is thrown into disarray by its fit to empirical patterns [8]. Here I explain this paradox in terms of the ecological equivalence realized by coexisting species at demographic equilibrium. Analyses and simulations of co-existence equilibria demonstrate the emergent property of ecological equivalence among species with a rich diversity of attributes, leading to novel predictions for a quantifiable gradation in species-area relationships between neutral and niche models.

A neutral model of empirical relationships eliminates “the entire set of forces competing for a place in the explanation of the pattern” [9]. Accordingly, HNT assumes that all species behave identically in a zero-sum game such that the total density of individuals in a trophically similar community remains constant regardless of species composition. The defining image of this ecological equivalence is a tropical forest canopy, with remarkably constant total densities of trees regardless of large regional variations in constituent species [1]. Interpretations of zero-sum equivalence routinely omit to distinguish between the equal vital rates realized at the system carrying capacity approximated in this image (and most datasets), and the intrinsic vital rates that define the heritable character traits of each species. Models of HNT consistently prescribe identical intrinsic rates and niche dimensions. Hubbell [1] anticipated the disjuncture between realized and intrinsic rates by comparing ecological equivalence to the fitness invariance achieved at carrying capacity, allowing for different trade-off combinations in life-history traits. The prevailing convention, however, remains that ecological equivalence explicitly requires symmetric species with identical per capita vital rates, thereby promulgating the notion that HNT is built on an unrealistic foundation [3].

Theoretical studies have sought various ways to reconcile neutral patterns with niche concepts. Intrinsically similar species can coexist under niche theory [7], and niches add stabilizing mechanisms that are absent under the fitness equivalence of intrinsic neutrality [10]. Comparisons of niche to neutral simulations in a saturated system of fixed total abundance have shown that they can predict similar species-abundance distributions (SADs) and species-area relationships [11], demonstrating that neutral patterns need not imply neutral processes [12]. Even neutral processes of intraspecific competition and dispersal limitation cannot be distinguished in principle for species-abundance predictions [13-16]. Here I use an analysis and simulation of Lotka–Volterra dynamics to model zero-sum ecological drift as an emergent property of stochastic niche structures at dynamic equilibrium. I explain its appearance in the steady-state distributions even of extremely dissimilar species in terms of the trivial expectation that species must achieve ecological equivalence at their co-existence equilibrium, which is defined by equal realized fitness for all. Although the predictions are standards of Lotka–Volterra analysis for a homogeneous environment, they drive

a simulation that for the first time spans across dispersal-limited neutral to stochastic niche scenarios without fixing the total abundance of individuals.

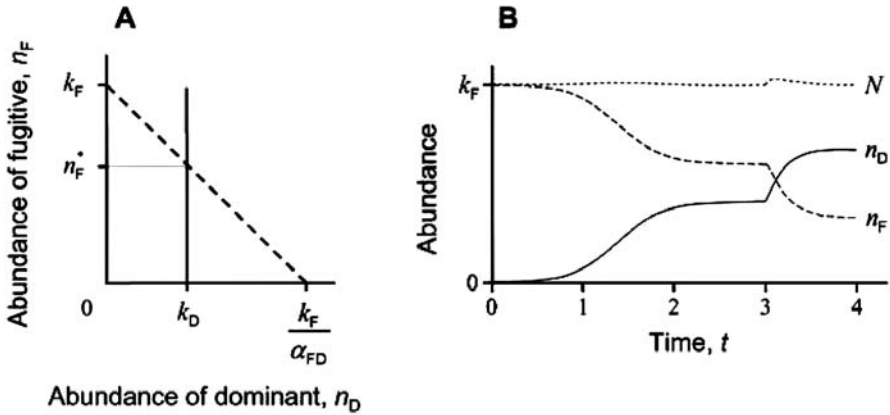
The neutral simulation developed here is consistent with the models of Solé et al. [17] and Allouche and Kadmon [18] in having total species,  $S$ , abundance of individuals,  $N$ , and zero-sum dynamics as emergent properties (in contrast to refs. [1, 11, 12, 19]). The  $S$  species are identical in all respects including interspecific interactions equal to intraspecific (in contrast to refs [13, 16]). Non-neutral simulations developed here extend the model of Chave et al. [11] by allowing competitive differences to vary stochastically on a continuous scale, as in Purves and Pacala [12]. They extend both these models by allowing pre-emptive recruitment and emergent zero-sum dynamics, and the model of Calcagno et al. [20] by adding dispersal limitation. They are consistent with Tilman's niche theory [21, 22] in their population abundances being a function of species-specific vital rates.

These simulations confirm the previously untested prediction [12] that colonization-competition trade-offs with stochastic colonization will exhibit zero-sum ecological drift and produce rank abundance curves that resemble neutral drift. Truly neutral dynamics should nevertheless sustain a lower total density of individuals at density-dependent equilibrium. This is because intrinsically identical species must interact as strongly between as within species. They therefore experience no competitive release in each others' presence, contrasting with the net release to larger populations obtained by segregated niches. The simulations demonstrate this fundamental difference, and I discuss its use as a signal for dynamic processes when predicting species-area relationships.

### Analysis of Abundance Patterns for Two-niche Communities

Species characterized by extremely different intrinsic attributes can achieve ecological equivalence in a zero-sum game played out at dynamic equilibrium. Take for example a two-species community comprising a dominant competitor displacing the niche of a fugitive (e.g., [23]). The fugitive survives even under complete subordination, provided it trades competitive impact for faster growth capacity [24]. Figure 1 illustrates the equal fitness, zero-sum outcome at density-dependent equilibrium under this most extremely asymmetric competition. The carrying capacity of each species is a function of its intrinsic lifetime reproduction (detailed in Materials and Methods Equation 1), and equilibrium population sizes are therefore a function of the species-specific vital rates. Regardless of variation in the ratio of dominant to fugitive carrying capacities,  $0 \leq k_D/k_F \leq 1$ , the system density of individuals is attracted to the stable equilibrium at  $N = n_F + n_D = k_F$ . Knocking out the fugitive reduces  $N$  to the smaller  $k_D$ , but only until invasion by another fugitive. This may be expected to follow rapidly, given the fugitive characteristic of fast turnover. The steady-state scenario is effectively neutral by virtue of the dominant and fugitive realizing identical vital rates and constant total density at their co-existence equilibrium despite contrasting intrinsic (heritable) rates. The reality that species differ in their life history traits therefore underpins the assumption of ecological equivalence, which then permits fitting of intrinsically neutral models with vital rates set equal to the realized rates. In the next section, these predictions are extended to simulate the drift of species invasions that sustains the dynamics

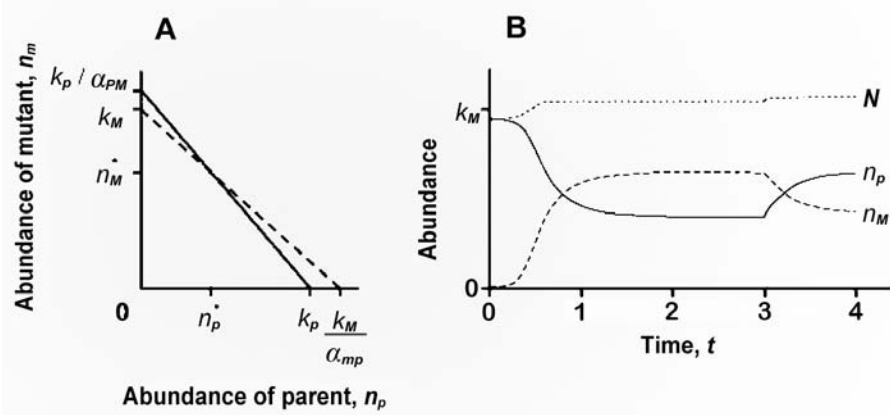
of recruitment following deaths and extinctions among multiple species of dominants and fugitives.



**Figure 1.** Equilibrium co-existence of a fugitive species invaded by a competitive dominant. With competition coefficients  $\alpha_{DF} = 0$ ,  $\alpha_{FD} = 1$ , the fugitive persists provided it has the greater carrying capacity:  $k_F/k_D > 1$ . (A) Lotka–Volterra phase plane with steady-state abundance at the intersection of the isoclines for the fugitive (dashed line) and the dominant (solid line). (B) Equilibration of abundances over time given by Runge–Kutta solutions to Equation 1, with a 20% drop in the dominant’s intrinsic death rate,  $d_D$ , imposed at  $t = 3$  (equivalent to a rightward shift in its isocline) to illustrate the constancy of  $N = n_F + n_D$ .

The same principle of trade-offs in character traits conversely allows a sexually reproducing species to withstand invasion by highly fecund asexual mutants [25, 26]. A 2-fold advantage to the mutant in growth capacity resulting from its production of female-only offspring is canceled by even a small competitive edge for the parent species (Figure 2). Sexual and asexual types coexist as ecological equivalents to the extent that each invades the other’s population to symmetric (zero) net growth for all. Although the dynamics are not zero-sum if the mutant has some competitive impact on the parent species, they approach it the higher the impact of parent on mutant and the faster its growth capacity (albeit half the mutant’s). Attributes such as these accommodate greater similarity between the types in their carrying capacities and competitive abilities, which aligns the two isoclines. A consequently reduced stability of the co-existence equilibrium may result in the sexual parent ousting the asexual mutant over time, for example if the latter accumulates deleterious mutations [26, 27].

These local-scale dynamics apply equally at the regional scale of biogeography, reconfiguring individual death as local extinction, and birth as habitat colonization [24]. Equally for regional as for local scales, rate equations take as many dimensions as species in the community, with their coupling together defining niche overlap [24, 28]. Co-existence of the species that make up a community is facilitated by their different heritable traits, which is a fundamental premise of niche theory. Ecological equivalence, and hence modeling by neutral theory is nevertheless possible by virtue of the co-existence equilibrium leveling the playing field to zero net growth for all.



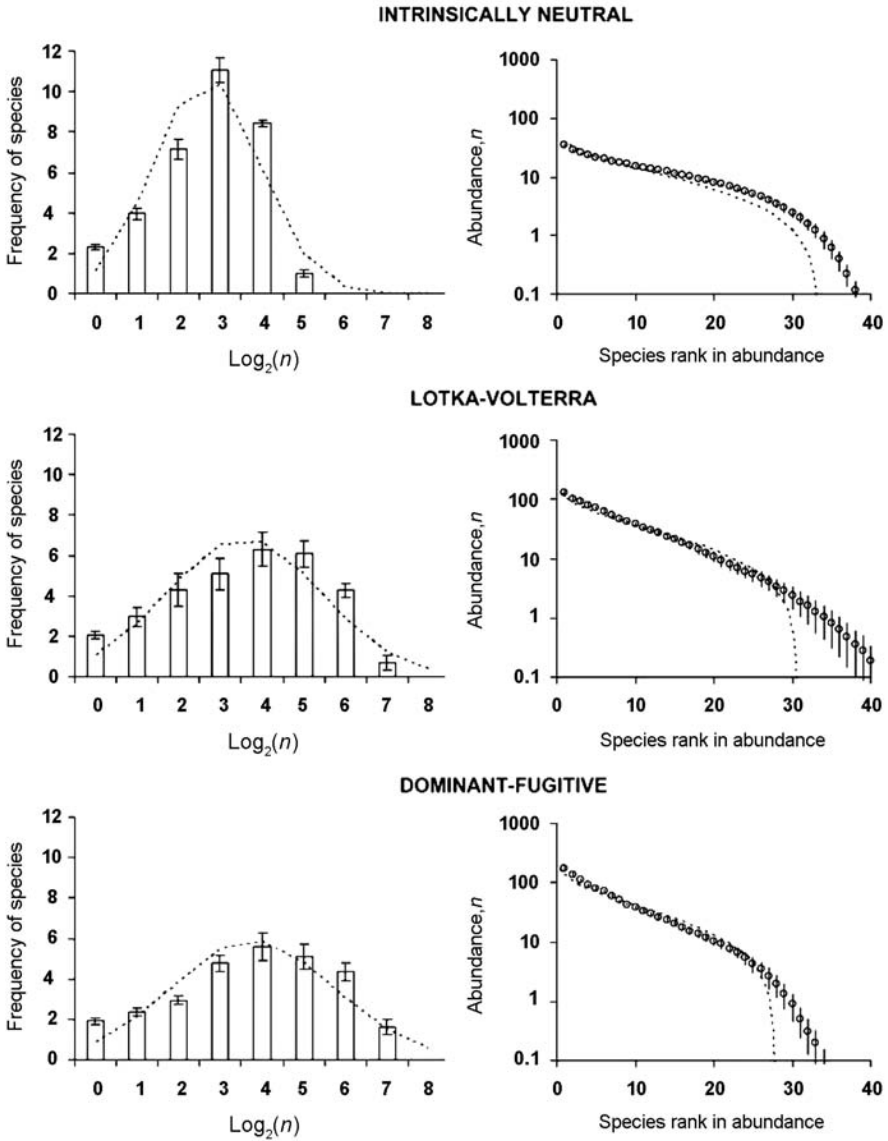
**Figure 2.** Equilibrium co-existence of a sexually reproducing parent population  $n_p$  invaded by an asexual mutant,  $n_m$ . With the mutant having identical vital rates except for twice the intrinsic propagation rate per capita:  $b_M = 2 \cdot b_p$ , the parent species persists if  $\alpha_{PM} < k_p/k_M$ . (A) Phase plane. (B) Equilibration of abundances over time given by Equation 1, with a 50% drop in the parent's intrinsic death rate imposed at  $t = 3$  to illustrate approximate constancy of  $N = n_M + n_p$ .

The above examples of dominant versus fugitive and sexual versus asexual were illustrated with models that gave identical realized rates of both birth and death at co-existence equilibrium. Fitness invariance and zero-sum dynamics, however, require only that species have identical net rates of realized birth minus death. The simulations in the next section show how neutral-like dynamics are realized for communities of coexisting species with trade-offs in realized as well as intrinsic vital rates.

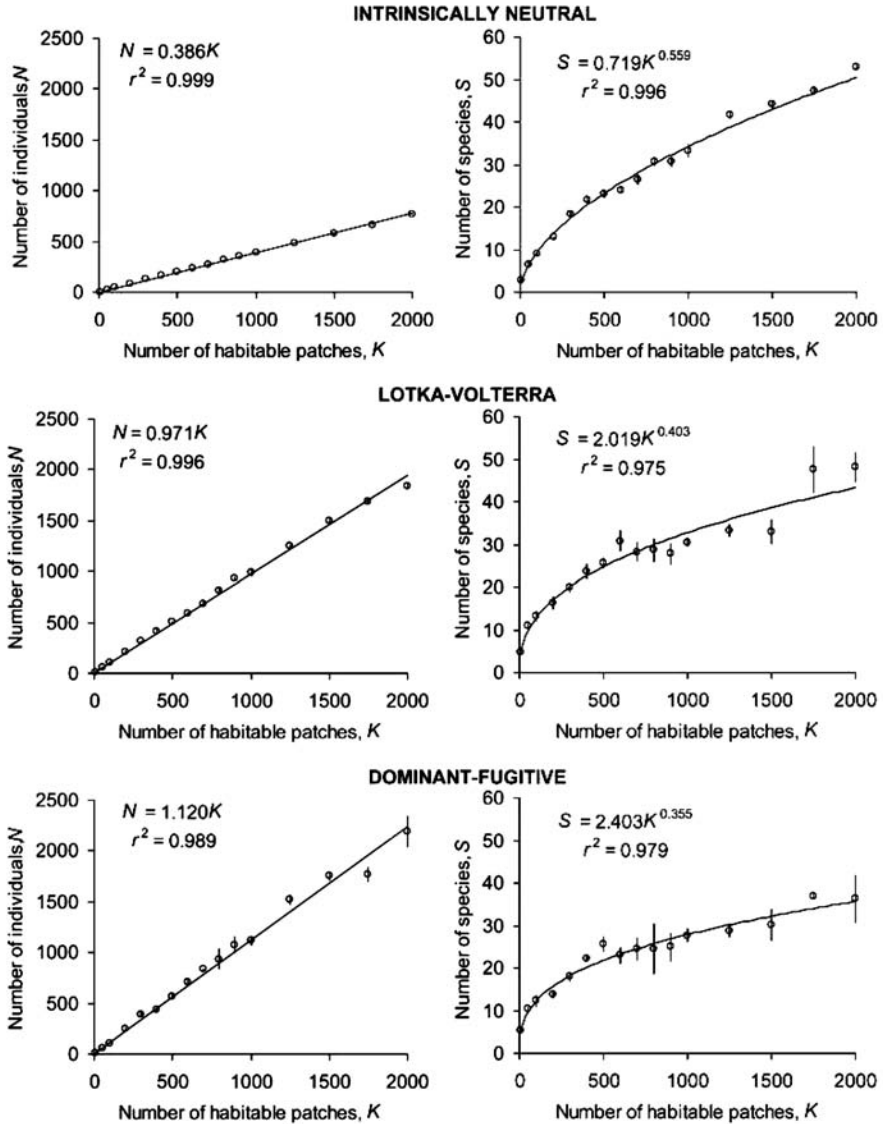
### Comparison of Simulated Neutral and Multi-niche Communities with Drift

Figure 3 illustrates the SADs and species-area relationships of randomly assembled  $S$ -species systems under drift of limited immigration and new-species invasions (protocols described in Simulation Methods). From top to bottom, its graphs show congruent patterns between an intrinsically neutral community with identical character traits for all species (equivalent to identically superimposed isoclines in Figures 1 and 2 models), and communities that trade growth capacity against competitive dominance increasingly starkly. The non-neutral communities sustain more total individuals and show greater spread in their responses, reflecting their variable life-history coefficients. Their communities nevertheless follow qualitatively the same patterns as those of neutral communities. For intrinsically neutral and niche-based communities alike, Figure 3 shows SADs negatively skewed from log-normal (all  $P < 0.05$ , every  $g_i < 0$ ), and an accelerating decline in rank abundances of rare species (cf. linear for Fisher log-series) that is significantly less precipitous than predicted by broken-stick models of randomly allocated abundances among fixed  $S$  and  $N$ ; Figure 4 shows constant densities of total individuals regardless of area (unambiguously linear), and Arrhenius relationships of species richness to area (unambiguously linear on log-log scales).





**Figure 3.** Simulated steady-states of species-abundance distributions (SADs). From top to bottom, graphs show average patterns for intrinsically neutral, Lotka–Volterra, and dominant-fugitive communities. The SADs each show mean  $\pm$  s.e. of six replicate communities with carrying capacity  $K = 1000$  habitable patches. Frequencies are compared to log-normal (left-hand column) and MacArthur’s broken-stick (right-hand column). See Materials and Methods for input parameter values and the process of random species assembly.



**Figure 4.** Simulated steady-states of species-area relationships (SARs). The SARs each show mean  $\pm$  s.e. of three replicate communities. See Materials and Methods for input parameter values and the process of random species assembly.

The extended tail of rare species seen in the Figure 3 SADs is caused by single-individual invaders replacing random extinctions of  $n$ -individual species. Further trials confirm that reduced dispersal limitation exacerbates the negative skew from the log-normal distribution, while sustaining a higher total density of individuals. The extinction-invasion imbalance sets the equilibrium species richness,  $S$ , as a power function

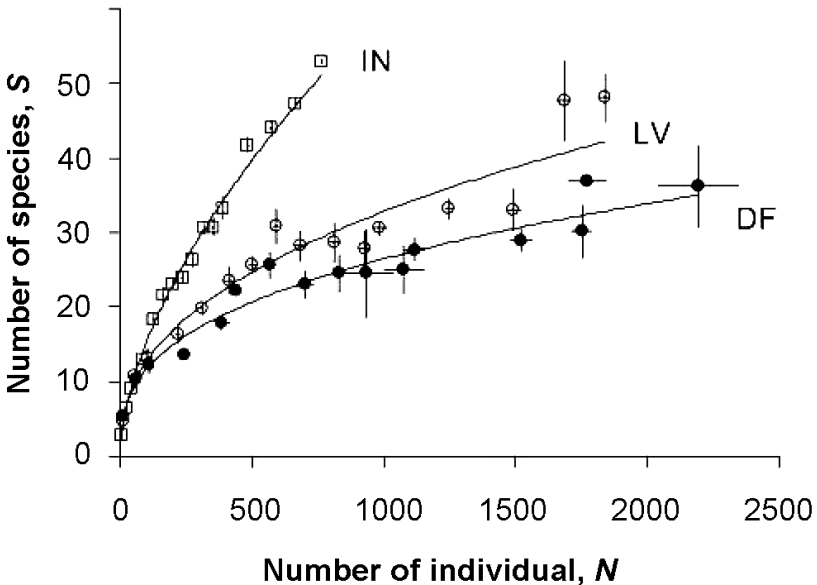
of total population density,  $N$ . This can be expressed as the Arrhenius relationship:  $S = cK^z$  (Figure 4 right-hand column) by virtue of the zero-sum relation of  $N$  to  $K$  (Figure 4 left-hand column). Further simulations show that reduced dispersal limitation raises  $c$  and reduces  $z$ , and a higher rate of new-species invasions raises  $c$  (though not  $z$ , in contrast to predictions from spatially explicit neutral models [29]).

The closely aligned proportionality of total individuals to habitable area for all communities illustrates emergent zero-sum dynamics for neutral and non-neutral scenarios (Figure 4 left-hand column). Despite sharing this type of pattern, and rather similar densities of species (Figure 4 right-hand column), the non-neutral communities sustain more than double the total individuals. This difference is caused by a more than halving of their competition coefficients on average (all  $\alpha_{ij} = 1$  for neutral, mean  $\alpha_{ij}$  ( $i \neq j$ ) = 0.45 for Lotka–Volterra, mean ratio of 0:1 values = 58:42 for dominant–fugitive). The zero-sum gradient of  $N$  against  $K$  is simply the equilibrium fraction of occupied habitat, which is  $1-1/R$  for a closed neutral scenario, where  $R$  is per capita lifetime reproduction before density regulation ( $b/d$  in Materials and Methods Equation 1 [23, 24]). The closed dominant–fugitive scenario modeled in Figure 1 has a slope of  $k_f/K = (1-1/R)/\alpha$ , where  $R$  and  $\alpha$  are system averages. Further simulation trials show the slope increasing with immigration, for example by a factor of 1.9 between closed and fully open (dispersal unlimited) Lotka–Volterra communities. Dispersal limitation therefore counterbalances effects of the net competitive release obtained in niche scenarios from  $\alpha_{ij} < 1$  (as also seen in models of heterogeneous environments [19]).

The less crowded neutral scenario sustains a somewhat higher density of species than non-neutral scenarios (comparing Figure 4  $z$ -values for right-hand graphs), and consequently it maximizes species packing as expressed by the power function predicting  $S$  from  $N$  in Figure 5. With no species intrinsically advantaged in the neutral scenario, its coefficient of power is higher than for pooled non-neutral scenarios (0.594 and 0.384 respectively, loglog covariate contrasts:  $F_{1,42} = 122.72$ ,  $P < 0.001$ ). The lower coefficients of Lotka–Volterra and dominant–fugitive scenarios are further differentiated by competitive asymmetry (0.412 and 0.355 respectively,  $F_{1,42} = 7.24$ ,  $P < 0.01$ ). In effect, the neutral scenario has the lowest average abundance of individuals per species,  $n$ , for a community of size  $K$  with given average  $R$ , which is also reflected in the modal values in Figure 3 histograms for  $K = 1,000$  patches.

The lower  $N$  and  $n$  predicted for the intrinsically neutral scenario point to a detectable signal of steady-state intrinsically neutral dynamics:  $\alpha = 1$  for all, because intrinsically identical species cannot experience competitive release in each others' presence (cf.  $\alpha_{ij} < 1$  in niche models). These interactions may be measurable directly from field data as inter-specific impacts of equal magnitude to intra-specific impacts; alternatively, Lotka–Volterra models of the sort described here can estimate average competition coefficients at an observed equilibrium  $N$ , given an average  $R$  (a big proviso, as field data generally measure realized rather than intrinsic vital rates). This distinction of intrinsically neutral from non-neutral dynamics has been masked in previous theory by the convention for neutral models either to fix  $N$  [1, 11, 12] or to set zero interspecific impacts [13, 16]. By definition, identical species cannot be invisible to each other unless they are invisible to themselves, which would require density

independent dynamics. Simulations of non-interacting species under density-dependent regulation therefore embody an extreme version of niche theory whereby each species occupies a unique niche, somehow completely differentiated by resource preferences rather than partially by trade-offs in vital rates. These models fit well to species abundance distributions in rainforests and coral reefs [13-16], though without providing any explanation for what attributes would allow each species to be invisible to all others (in contrast to the trade-off models). Indeed the condition is unrealistic at least for mature trees that partition a homogeneous environment by each making their own canopy. This so-called neutral scenario ([13, 16], more appositely a neutral-niche scenario) has no steady state outcomes in the analyses and simulations described here, because setting all  $\alpha_{ij} = 0$  ( $i \neq j$ ) allows indefinite expansion of  $S$  and hence also of  $N$ . A slightly less extreme neutral-niche community is modeled by setting all interspecific impacts to a common low value. Simulations at  $\alpha_{ij} = 0.1$  for all  $i \neq j$  give a zero-sum relation  $N = 4.026K$ , which has >4-fold steeper gradient than that for the Lotka-Volterra scenario (Figure 4) reflecting its >4-fold reduction in  $\alpha$  and consistent with its representation of a highly niched scenario.



**Figure 5.** Simulated steady-state relationships of species to individuals. Each point shows the mean  $\pm$  s.e. of the three replicate communities in Figure 4, and regression lines on the means are the power functions for intrinsically neutral (top) Lotka-Volterra (middle) and dominant-fugitive (lower) scenarios.

## DISCUSSION

Although intrinsic identity is clearly not a necessary condition of ecological equivalence or of zero-sum abundances at dynamic equilibrium, only neutral models sustain

these outcomes over all frequencies. It is their good fit to steady-state patterns of diversity and abundance even for communities subject to species turnover in ecological drift that has argued powerfully for niche differences having a limited role in community structure. The Figure 3 simulations reveal these types of patterns to be equally well represented by niche models, however, despite constituent individuals and species achieving fitness equivalence only at dynamic equilibrium. Non-neutral dynamics of a mature community express the community-wide average of fluctuations either side of equilibrium. Outcomes regress to the equilibrium mean for a random assembly of species undergoing stochastic extinctions of rare members, regulated by spatially autocorrelated immigration, and replacement by initially rare invaders. The predicted power of neutral theory can be taken as evidence for ecological equivalence at the co-existence equilibrium of species with more or less different intrinsic attributes.

Modeling zero-sum ecological drift as an emergent property reveals a key distinguishing feature of truly neutral communities. Their intrinsically identical species self-regulate to a lower total density as a result of inter-specific impacts equaling intra-specific impacts. Any empirical test for competitive release is therefore also a test for niche structure. For example, removing habitat is predicted to give a relative or absolute advantage to species towards the fugitive end of a dominant-fugitive spectrum, which may be picked up in correlated life-history traits for winners or losers under habitat loss or degradation [23, 24]. In contrast, neutral dynamics lead to sudden biodiversity collapse at a system-wide extinction threshold of habitat [17]. The extinction threshold of habitat for a resource-limited metapopulation is set by the fraction  $1/R$  [30, 31]. The value of  $R$  is thus an important yardstick of resilience in conservation planning. A neutral model fitted to empirical zero-sum abundances will overestimate their community-wide  $R$ , and hence overestimate community resilience, if  $\alpha_{ij}$  are overvalued by setting all to unity. Likewise, a neutral model that sets all  $\alpha_{ij} = 0$  ( $i \neq j$ ) will underestimate  $R$ , and hence resilience, if the  $\alpha_{ij}$  are undervalued by setting all to zero.

Ecological equivalence is a much more permissive requirement for neutrality than is currently acknowledged in theoretical developments on HNT. Co-existence equilibria largely achieve the neutrality-defining mission, to eliminate all of the forces competing for a place in explanations of pattern. It remains an open question whether they do so best among species with most or least competitive release in each others' presence (e.g., Figure 1 versus Figure 2 respectively, and Figure 3 dominant-fugitive versus Lotka-Volterra respectively; [7, 10, 32]). Models need to incorporate the ecologically realistic dynamics of interspecific interactions simulated here in order to explore the true nature of competitive release between extreme scenarios of niches that are all intrinsically identical (HNT [1]) and intrinsically unique [13], [16]. Simulations of niches distributed along environmental gradients have found emerging groups of intrinsically similar species over evolutionary timescales [33]. For the spatially homogeneous environments modeled here, competition-recruitment trade-offs will always sustain species differences. In their absence, however, homogenous environments will tend to favor fast-recruiting competitive dominants. This species type may eventually prevail, with runaway selection checked by other forces such as predation, disease, mutation accumulation, and environmental variability. These systems would merit further study because many of their attributes could be those of intrinsically neutral dynamics.