

Biodiversity: From evolutionary origins to ecosystem functioning

David Tilman^{1,2}

¹Department of Ecology, Evolution and Behavior, University of Minnesota, MN, USA.

²Bren School of Environmental Science and Management, University of California, Santa Barbara, CA, USA

Correspondence:

David Tilman
Department of Ecology, Evolution
and Behavior
University of Minnesota
St. Paul 55108, MN, USA

E-mail: tilman@umn.edu

Summary. How the Earth came to have on the order of 10 million species and the impacts of this biodiversity on ecosystems, are long-standing questions in evolution and ecology. I propose that both the evolutionary causes and the ecological consequences of biodiversity share a common origin—unavoidable tradeoffs that organisms face when dealing with multiple limiting factors. Our grassland biodiversity experiments and studies in many other systems have shown that species diversity is a major determinant of ecosystem productivity, stability, invasibility and nutrient dynamics. The preservation, conservation and restoration of biodiversity should be a high global priority. Indeed, the evidence accumulated over the past two decades suggests the long-term persistence of a species in an ecosystem should be taken as *prima facie* evidence that the species contributes to the functioning of that ecosystem. [Contrib Sci 11:11-20 (2015)]

The most unique feature of Earth is the existence of life, and the most profound aspect of this life is its amazing diversity. Indeed, the fossil record shows that, after life's initial emergence, there has been a seemingly unending increase in the global number of plant and animal species, as is clearly shown by Benton's [5] summary of the number of families of terrestrial plants and animals (Fig. 1). Recent estimates are that the Earth now has on the order of 10 million species. This remarkable biodiversity fascinated and puzzled the great naturalists, including Darwin and Wallace. An enduring mystery, highlighted in G. E. Hutchinson's classic paper, raised the issue of how so many different species could compete

with each other and still coexist [30]. This mystery inspired my early work on competition and coexistence of species of algae [57,58], and has remained an interest of mine ever since [47,50,55,56].

Earth also has more than 7,000 million people, with global population being estimated to reach almost 10,000 million people within 50 years, and perhaps 11,000 million people by the end of this century. Global food demand impacts the natural ecosystems of Earth by causing land clearing that simplifies environments. At present, almost half of Earth's ice-free land surface has been converted into agricultural lands, which have much lower species diversity

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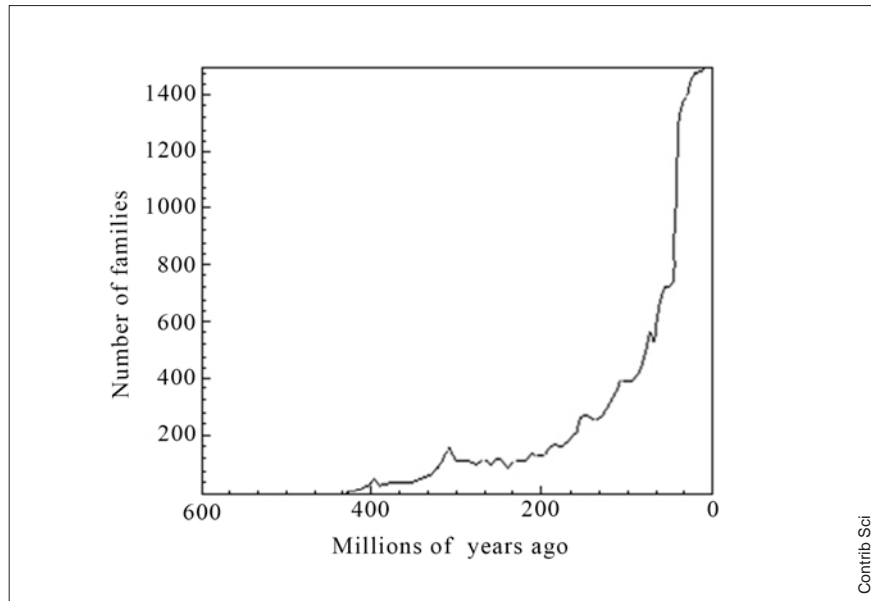


Fig. 1. The number of families of land-based (non-marine) plants and animals observed in the fossil record from the Ordovician era, about 450 million years ago, to the present time. This long-term accumulation of families is mirrored by genera within each family, and by species within genera. Figure modified from Benton [5].

than the natural ecosystems from which they were derived. Concerns about such simplification led to multiple studies on the possible impacts of biodiversity loss on the stability and functioning of ecosystems [11,42,44,63].

In this paper, I discuss why it may be that the Earth came to have such great biodiversity, the effects of biodiversity loss on the functioning of ecosystems, and why the processes that control speciation may also shape biodiversity's impact on ecosystem functioning.

The coexistence paradox and biodiversity

As Hutchinson [30] highlighted, then-current ecological concepts and models could not explain how so many species could compete and still coexist when limited by a small number of resources. In particular, at that time, the conceptual expectation was that the number of coexisting species could never exceed the number of resources for which they were competing. Subsequent experiments and theory have solved this mystery [2,34,43,52,54,57]. Theory now predicts that a potentially unlimited number of species, competing for just two limiting resources, can stably coexist if: (1) their habitat is spatially, or temporally, heterogeneous;

and (2) if interspecific tradeoffs cause progressively superior competitors for one resource to necessarily be progressively poorer competitors for other limiting resources [56].

Let us consider competition for two nutritionally essential resources. For instance, of the two species illustrated in Fig. 2A, species A is the best competitor for resource 1 (R1), and the poorest for R2, and species B is the best competitor for R2, but the poorest for R1. As shown, there are a range of habitat conditions (supply rates of the two resources that are in region H2) for which these two species stably coexist [56]. Many more than just two species can coexist when limited by two resources as long as all of the species are bound to the same interspecific tradeoff curve (Fig. 2B) and the habitat has spatial heterogeneity in the supply rates of the two resources. Indeed, under these conditions, there is no simple mathematical limit to the number of coexisting species. Rather, resource competition theory predicts that as many species can coexist as there are points on a line segment [56].

Many other types of interspecific tradeoffs can also lead to the coexistence of large numbers of competing species. For instance, an interspecific tradeoff between the ability to locally compete for a single limiting resource, versus the ability to disperse to open sites, is predicted by a series of differential equations to allow a potentially unlimited number of species to coexist [52]. A tradeoff between the ability to compete for

a single limiting resource at different temperatures can, when generalized to a suite of any number of competing species, allow all such species to persist in a habitat that is spatially heterogeneous in temperature. Tradeoffs for other limiting factors can be similarly described [34,56]. Multi-trophic-level tradeoffs, such as a tradeoff between the ability of species to compete for a limiting resource, versus their resistance to predation, can also allow more species to coexist than there are limiting resources [33,56]. However this tradeoff-based mechanism of coexistence does not require the assumption of spatial, or temporal, heterogeneity. Finally, one of the more interesting models of coexistence is based on oscillations in resource availabilities, and the mechanisms whereby such oscillations can allow many more species to coexist than there are resources [2,3,27,34]. Coexistence in these types of models also requires tradeoffs. In these cases, the tradeoffs are between the ability of species to compete in unvarying, equilibrational habitats, versus their ability to compete when resources oscillate.

Based on these and other advances in ecological theory, and on experimental confirmation of the predictive abilities of some of these theories, Hutchinson's paradox of diversity has been resolved. However, to date, there have been few empirical demonstrations of the actual limiting factors in ecosystems, and of the occurrence of appropriate tradeoffs among a majority of the co-occurring species. Thus, we do not yet know if simple tradeoffs among a few limiting factors truly do explain the local and regional coexistence that we observe, or if only high-dimensional tradeoff surfaces, defined by a large number of limiting factors, can explain the high local species diversity observed in so many of the world's terrestrial and aquatic ecosystems. Until we know why so many species coexist, it will be difficult to predict how a variety of anthropogenic environmental changes, such as nutrient pollution, loss of top predators, or loss of herbivores, will impact plant diversity.

Perhaps the most perplexing aspect of coexistence theory is the requirement for strict interspecific tradeoffs. If any species could overcome an existing interspecific tradeoff, it should displace established species, as shown for species F (Fig. 2C) that would displace species B and C. Moreover, once such a truly superior species appeared, it could become the

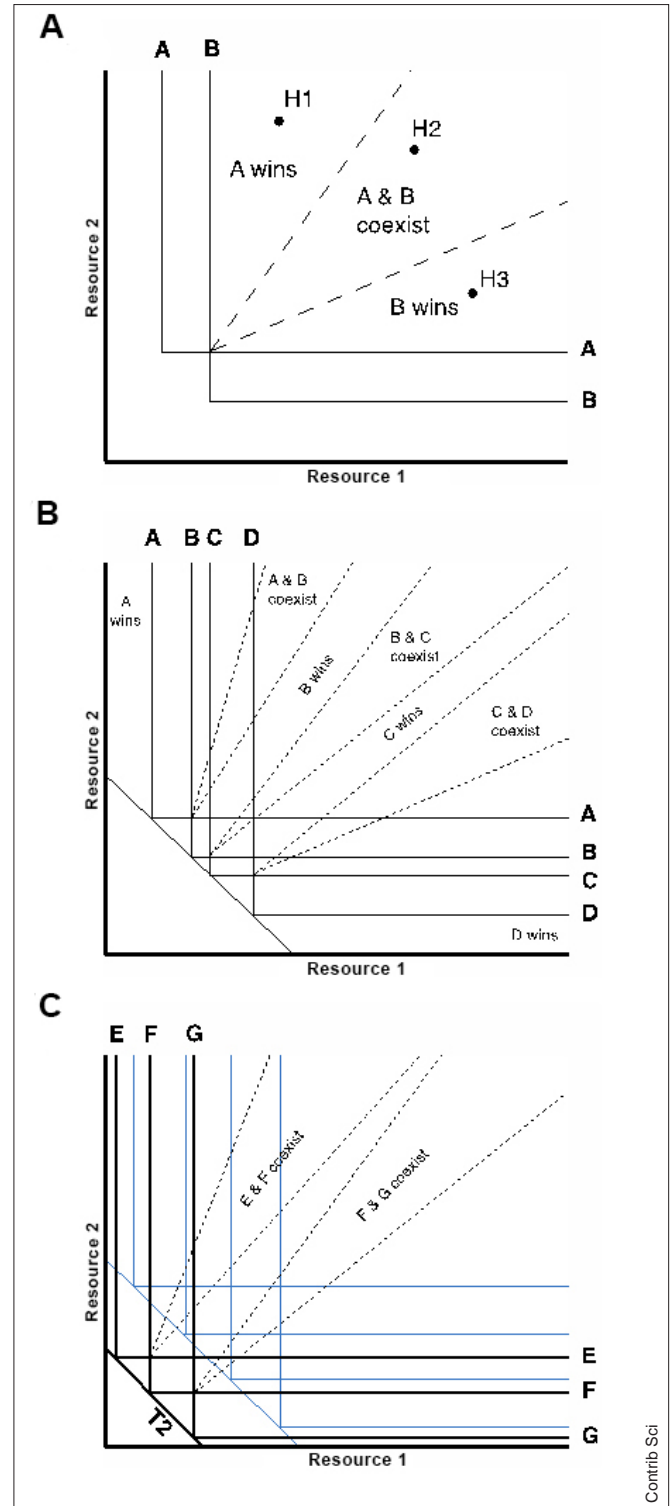


Fig. 2. (A) Competition for 2 resources by two species that have a tradeoff in their abilities to compete for the two resources. (B) The ability of two species to locally coexist at sites with appropriate amounts of two resources, and for many species to coexist in a habitat with spatial heterogeneity in two resources, if they are all bound to the same tradeoff surface, T1. (C) Invader with a superior tradeoff (T2) displaces species from an inferior tradeoff curve (T1). T2 is a superior tradeoff curve since the species on it (species E, F and G) can consume resources down to, and survive at, lower levels of R1 and R2 than can the species of T1 (species A, B, C and D, as in part B).

progenitor of a radiation that created a suite of new species whose emergence would define a new and competitively superior tradeoff curve, as indicated by the T2 tradeoff curve. This new taxonomic guild (species E, F and G; Fig. 2C) would competitively displace the pre-existing species that had radiated along the T1 tradeoff curve (species A, B, C and D). Displacement occurs because species on the T2 tradeoff curve drive R1 and R2 to levels lower than the minimal levels required for the survival of the T1 tradeoff curve species [56].

Tradeoff-based competition theory thus makes an interesting set of predictions about evolution and speciation. If all existing species, and all potential future species, are bound to the same tradeoff curve (or, more realistically, multi-axis tradeoff surface), then the formation of a new species should not lead to the competitive displacement of any existing species. In this case, coexistence would be the rule. In contrast, if natural selection led to the gradual accumulation of truly superior suites of traits that exceeded the bounds of an existing tradeoff surface, the net result would be that the formation of new species caused the competitive displacement of established species.

Species formation, diversification and tradeoffs

What does the fossil record tell us about speciation and the occurrence of coexistence or displacement? The diversification of terrestrial and marine plants and animals that occurred from the Cambrian era (about 550 million years ago) to the modern era has been massive. There are now more than 2500 different families of terrestrial (Fig. 1) and marine plants and animals arose, which contain millions of species. A major feature of this long period of diversification is coexistence. In particular, the arrival or emergence of new families and species was rarely associated with the loss of existing families or species [14,61,62]. Rather, the newly emerging taxa have often coexisted for millions of years with the pre-existing species of their biogeographic realm. Indeed, in their review of patterns of species radiations, Benton and Emerson [4] asserted that there was “no evidence that rapidly speciating clades have reached a limit, nor that they are driving other clades to extinction.”

Why was coexistence, rather than competitive displacement, the norm? In discussing the diversification of the tetrapods, Benton [5] noted that the new families and species were differentiated from the established species by having ecological attributes that allowed them to exploit diets

and habitats not previously used by tetrapods. Expressed differently, the new taxa had tradeoff-based differences that let them excel in ecologically empty sites, even though the traits that allowed this also precluded them from performing well in sites already occupied by their progenitors. Analysis of 840 families within the tetrapods showed that these taxa had only minor overlaps in their habitat type, diets, body size and geographic realms [5]. This suggests both that their diversification involved the acquisition of traits that allowed them to use underexploited resources and/or habitats, and that the cost of these traits was that new taxa were no longer capable of persisting in the ecological roles of their progenitors. This latter fact, which is easily overlooked, is the ecological signature of the tradeoffs that occur during speciation.

The major biogeographic realms of the Earth have had geologically long periods of isolation during which speciation within each realm generated its own unique floras and faunas. Given these long periods of separate and distinct species radiations, it is interesting to ask what happens when the formation of land bridges allows movement of terrestrial animals and plants between two realms, or when changes in sea levels and currents allows such movements between otherwise isolated ocean basins.

A summary and synthesis of major migrations between realms shows that species that move into new realms coexist with the established species of the new realm for millions of years [47]. If extinctions eventually occur, they are most often attributed to climatic change or to a mass extinction event, such as the Pleistocene extinctions of large mammals in Asia, Europe and the Americas. Whether considering invasions by plants [39,41], mammals [5,6,15,61,62] or mollusks [59], the consistent pattern of coexistence of resident and invading species and its great duration suggests the surprising hypothesis that all ecologically similar taxa are bound to the same tradeoff surface independent of their phylogenetic origins and the length of time that they evolved in different realms.

This “universal tradeoff hypothesis” thus suggests that intraspecific and interspecific tradeoffs are evolutionarily unavoidable, and that, at least since the Ordovician, the process of evolution and formation of new taxonomic lines and species has been characterized more by movement along an unavoidable tradeoff surface than by the emergence of truly superior combinations of traits, much as suggested for tetrapods [5].

The possible cause or causes of evolutionarily unavoidable tradeoffs merit consideration and debate. They might result from the universal cellular biochemistry and molecular genetic infrastructure that was created during the first 2000 million

years of evolution. All animals are derived from the same single eukaryotic cell, just as all higher plants are derived from the same single eukaryotic algal cell. As such, the differentiation of these cell lines into multicellular organisms would present a series of tradeoffs that carried costs and benefits. After all, any amino acid allocated to make one protein cannot be allocated to make a different one. Any cell dedicated to one purpose, such as motility, cannot be allocated to digestion or some other function. Thus, whether at the level of the metabolic specializations of cells within an individual or at the level of the functioning of physiological systems such as circulatory, or reproductive, or cognitive systems, allocation to one system decreases the proportional allocation to another system. Finally, even allocation to greater body size, and even if it could occur without changing the proportion allocated to different systems (which cannot occur for structural and other reasons), has costs, such as decreased maximal reproductive rates and specific growth rates.

Biodiversity and ecosystem functioning: a brief history

Let us now consider how the biological diversity of an ecological community or ecosystem might influence its functioning. Darwin [9] was perhaps the first naturalist to suggest that life's diversification had caused increased productivity in ecosystems [23]. A hundred years later Elton [12] proposed that greater species diversity was associated with greater stability, lower disease incidence, and lower rates of invasion by exotic species. These proposed effects of biodiversity on community and ecosystem processes, which has been based on the observations of two great naturalists, fell out of favor in the 1970's as the discipline of ecology started to become a more experimental and theory-based science. In essence, the lack of experimental or quantitative observational evidence, and the seeming logical contradiction of hypothesized mechanisms with the theory of evolution [18], combined with the seeming contradiction with new theoretical predictions [36], led most ecologists of that era to lose interest in the possible impacts of species diversity on community and ecosystem functioning. Instead, the discipline started exploring the mechanisms of interactions among species and the magnitudes of such interactions in natural ecosystems.

By the 1990's, after about two decades of work on such mechanisms, the discipline began to once again consider the possibility that the number of species might impact ecosystem

functioning [37,44]. The following year, two papers appeared in rapid succession in *Nature*. The first of these used results from 207 grassland plots that differed in plant diversity mainly because of different rates of nitrogen addition. It showed that plots with low plant diversity were much less stable during a severe drought than those with many plant species, and that this effect remained highly significant even after statistically controlling for a large number of potentially confounding variables [53]. The second paper presented the results of a growth chamber experiment in which the plant (and invertebrate) species numbers led to higher primary productivity [40].

As might be expected, this seeming support for a hypothesis that had been rejected in the 1970's was met with considerable questioning [1,10,19,28,29,60]. However, a large number of experimental tests were done across a variety of types of organisms and ecosystems, especially grasslands. As discussed below, the combined weight of these experiments and of theory built on the mechanisms of species interactions led to the emergence of a new paradigm.

Results of biodiversity experiments

It had been clear to us as soon as we did the analyses [53] that only a well-replicated and fully randomized field experiment could rigorously determine the effects of biodiversity on ecosystem functioning. Thus, in the summer of 1993, we prepared and laid out plots at the Cedar Creek Ecosystem Science Reserve for a biodiversity experiment, which we planted in the spring of 1994. The experiment had large plots (13 m × 13 m; later reduced to 9 m × 9m because of lack of sufficient research funds), with about 35 replicates at each of 5 levels of plant diversity (1, 2, 4, 8 and 16 plant species). The species composition of each plot was determined by a separate, random draw of species from a pool of 18 perennial plants that is common in nearby prairie grasslands and savannas. Plots were randomly located within the experimental grid. Randomization allowed us to average across the effects of various species combinations and thus to separate out effects attributable to species composition from those attributable to plant diversity.

Because of my involvement in it, the following discussion will focus on the Cedar Creek biodiversity experiment. It has revealed that plant biodiversity has unexpectedly strong impacts on many community and ecosystem processes. Annual net primary productivity, measured as the amount of aboveground biomass produced each year, has been a

significantly increasing function of plant species numbers from the first year that the plants reached maturity (1996), and on (Fig. 3A). Interestingly, the effect of diversity on productivity has become progressively stronger through time, with the average of the 16 species plots being about 70% more productive than the average of the monocultures the first year of measurement, but becoming >200% more productive by the 15th year, and on (Fig. 3A). In addition, the experiment clearly demonstrates what is called transgressive overyielding, which is considered the strongest evidence for demonstrating that the greater productivity of the higher diversity treatments is caused by interspecific complementarity and niche differentiation. As shown in Fig. 3B, the productivity of the most productive species in monoculture is less than that of the average 16 species mixture. Indeed, by 2012 the average 16 species plot had productivity that was much greater than the best monoculture species, and every individual 16-species plot was more productive than the best species in monoculture.

The Cedar Creek biodiversity experiment has also shown that greater plant diversity leads to greater year-to-year stability of net primary productivity [49]. This finding confirms the earlier comparative evidence that suggested that greater plant diversity led to greater stability of primary productivity [53]. Some other findings are insightful in their own right, and provide mechanistic insight into why net primary productivity increases with plant diversity, and why this effect becomes greater through time. Perhaps most important are the greater increases in soil organic carbon and soil organic nitrogen (Fig. 3C) observed in the higher diversity treatments [16,17,48]. These increases mean that soils of higher diversity treatments became progressively more fertile through time, with the greatest increases in soil fertility occurring at higher diversity. Greater productivity at higher diversity was also the result of greater consumption of the major limiting resource, soil nitrate [51], lower incidence of species-specific plant diseases [38], and shifts in the insect community toward higher levels of predatory and parasitoid insects and lower densities of herbivorous insects [20].

Another major finding of the Cedar Creek biodiversity experiment was that greater plant diversity led to lower rates of invasion by exotic plant species [13]. Why did this occur? Two lines of evidence support the hypothesis that plant invasions mainly occur when invaders are able to germinate, survive and grow on the amounts of limiting resources left unconsumed by the established plant species. In particular, lower levels of unconsumed soil nitrate of the higher diversity treatments greatly inhibited potential invaders [13]. In addition, the pattern of resource reduction by each of

three functional groups (cool season grasses, warm season grasses, and non-legume forbs) had its greatest inhibitory effects on invading species within that same functional group [13]. Thus the ecology of invasive species is, to a great extent, determined by their abilities to live on “leftover” resources.

A variety of meta-analyses that used results from the Cedar Creek experiment combined with results from many other biodiversity experiments, including experiments on other types of species and habitats, have found that the effects that we have observed at Cedar Creek are quite general [8,22,24,26]. The only seeming exception is an interesting one: results of shorter-term experiments are rarely as strong as those of longer-term experiments [7]. Our biodiversity experiments suggests that this may occur because of biodiversity-dependent feedback effects, such as increases in soil fertility and shifts in foodweb structure, that gradually magnify the strength of biodiversity effects. Because natural communities have existed for immensely longer periods of time than even the longest-running biodiversity experiment, it is important that current experiments continue, and that we place the greatest emphasis on long-term results.

How important is biodiversity?

Many other long-term experiments have been established at Cedar Creek Ecosystem Science Reserve, from 1982 and on, to determine the effects of factors that might influence plant species compositions or productivity in our perennial grassland ecosystems. In particular, we established randomized and replicated experimental additions of major limiting soil resources, including nitrogen, phosphorus, potassium, calcium, trace metals, and water, and other experiments with herbivore removal, or with different fire frequencies, or with carbon dioxide enrichment. A comparison of the effects of biodiversity with the effects of each of these other variables showed that none of these other variables had a larger impact on net primary productivity than biodiversity [46]. An analysis and synthesis of other experiments by Hooper et al. [25] led to a similar conclusion. Biodiversity is thus at least as important as nitrogen, water, herbivory, fire and carbon dioxide in determining ecosystem primary productivity, a finding that few scholars would have anticipated in the 1990's.

Two other studies highlight the strength and ubiquity of the effects of biodiversity. Isbell et al. [31] found that the loss of plant diversity caused by nitrogen addition led to subsequent loss of productivity. Indeed, after an initial increase in primary productivity that was strongly correlated

with the annual rate of nitrogen addition, productivity decreased through time in direct proportion to the greater loss of plant species numbers caused by higher nitrogen addition rates. Second, Hautier et al. [21] examined the stability of primary productivity across the full suite of different long-term experimental manipulations at Cedar Creek, and found a surprisingly simple explanation for the effects of fire, herbivory, water addition, drought and nitrogen addition on stability. The effect of each of these variables on the stability of primary productivity was explained by how that factor changed plant diversity. The quantitative effect on stability of each lost or gained plant species was identical to that observed in the Cedar Creek biodiversity experiment. In total, the effects of biodiversity are highly general. They apply just as rigorously when other factors, such as those associated with human-driven environmental change, cause the loss of diversity as when diversity is manipulated directly.

Theory of biodiversity and ecosystem functioning

As already discussed, numerous competing species are predicted to stably coexist if species have interspecific tradeoffs in their abilities to compete for resources and if the habitat is spatially and/or temporally heterogeneous. Such models became the foundation upon which to build modern theories of biodiversity effects on community and ecosystem processes. A review of five such models showed that all five predict that greater plant diversity leads to both greater primary productivity and to more complete use of the limiting resources [45]. These five models are based on five different mechanisms of competition, including competition for two essential resources [52]; for a single limiting resource in a spatial ecosystem [35]; for a single resource when temperature fluctuates [32]; for a two-dimensional niche space [52]; and for a single resource that is divided up among species via a modified broken-stick process [32]. All five models also predict that the temporal stability of primary productivity will be an increasing function of plant diversity [45].

Synthesis

The work I have summarized suggests an intriguing possibility—that the same forces and factors that led to the emergence of global biodiversity also necessarily make biodiversity be a major determinant of ecosystem functioning. Several lines

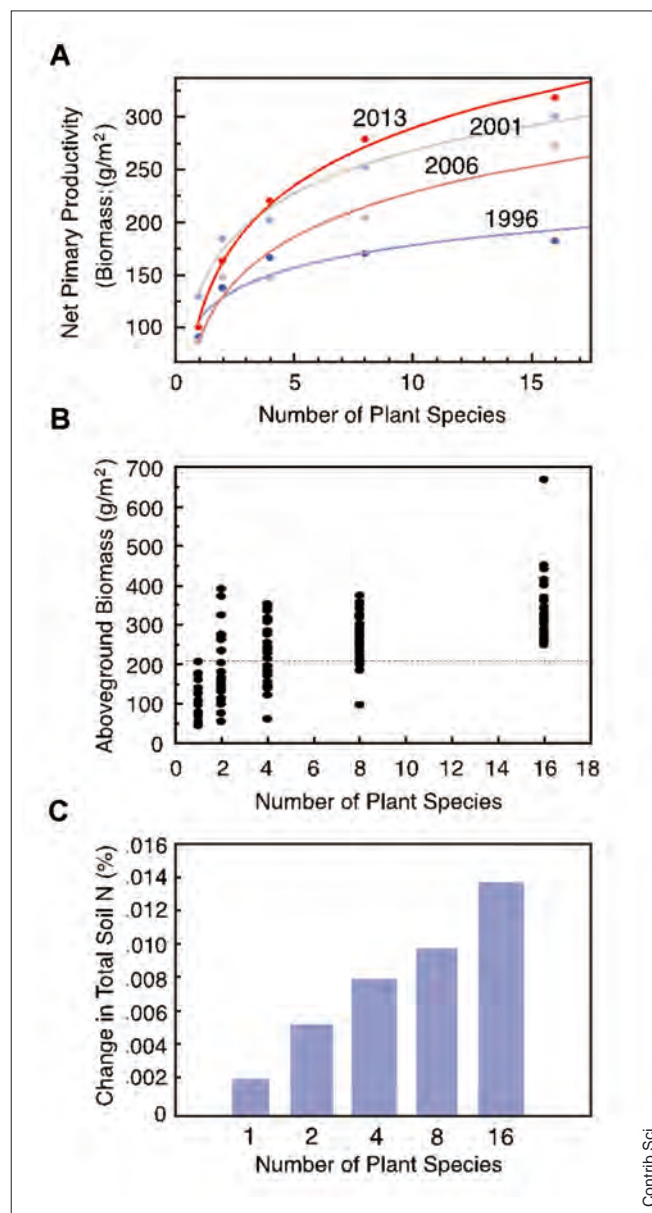



Fig. 3. Results from the Cedar Creek biodiversity experiment. **(A)** Plant productivity is an increasing function of the number of planted species each year of the experiment, and has tended to increase through time in the experiment. **(B)** On average for 2011–2013, primary productivity in the most productive species growing in monoculture (value indicated by dotted line) is much less than for the 16-species plots. **(C)** Total soil nitrogen content (mainly organic forms of nitrogen) increased through time most in higher diversity plots from 1994 to 2006 [16,17].

of evidence suggest that the diversification of higher plants and animals was a direct result of unavoidable tradeoffs. Such tradeoffs meant that new species did not competitively displace existing species, but rather were differentiated from them in ways that allowed coexistence when living in the same realm. Theory based on such tradeoffs predicts that

ecosystems containing more species will be more productive, more stable, less susceptible to disease, and less easily invaded. Numerous biodiversity experiments have found just such results.

This suggests that the long-term coexistence of a suite of plant species in an ecosystem may be evidence that each of those species contributes, in some way, to the functioning of the ecosystem. Clearly, this is a difficult hypothesis to directly test for each and every plant species, but the work reviewed above necessitates that this is the best-founded assumption that one should make in the absence of rigorous evidence to the contrary.

The conservation of Earth's biodiversity is thus of paramount importance to the functioning of the numerous terrestrial, freshwater, and marine ecosystems upon which the quality of human life is based. 

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About the author

David Tilman is director of the Cedar Creek Ecosystem Science Reserve long-term ecological research station, Regents Professor and McKnight Presidential Chair in Ecology at the University of Minnesota, professor at the University of California, Santa Barbara's Bren School of Environmental Science & Management, and instructor in conservation biology, ecology, evolution, behavior and microbial ecology. He obtained his B.S. in zoology in 1971 and his Ph.D. in ecology in 1976, by the University of Michigan with the study of the mechanisms of competition and coexistence among freshwater phytoplankton of Lake Michigan. His research focuses on both terrestrial and aquatic ecology, and he has developed his stochastic niche theory offering a new approach to ecological issues and removing former ecological paradigms. His long-term experiments have been of extreme importance in the understanding of the ecosystems' dynamics. In 2000 he was designated the Most Highly Cited Environmental Scientist of the Decade by Essential Science Indicators and, in 2002, he was elected to the US National Academy of Sciences. He

is also a fellow of the American Association for the Advancement of Science and of the American Academy of Arts and Sciences. Other awards include the 2010 Dr. A.H. Heineken Prize for Environmental Sciences, the 2014 International Balzan Prize for basic/applied Plant Ecology.



Fig. 4. Prof. David Tilman.



Scientists awarded the Ramón Margalef Prize for Ecology (2005-2014)

The Autonomous Government of Catalonia created the Ramon Margalef Award for Ecology to honor the memory of the Catalan scientist Ramon Margalef (1919–2004), one of the main thinkers and scholars of ecology as a holistic science. His contributions were decisive to the creation of modern ecology. This international award recognizes those people around the world who have also made outstanding contributions to the development of the science of ecology. More information can be obtained at: www.gencat.cat/premiramonmargalef.

Year	Winner	Main topic of research	Country
2005	Paul Dayton	Population and community ecology, mostly in benthic environments.	USA
2006	John Lawton	Dynamics of populations and communities, impact of global changes in organism populations and communities.	UK
2007	Harold A. Mooney	Plant physiological ecology and phenomena affecting global changes, such as ecological invasions, the loss of diversity and the degradation of ecosystems.	USA
2008	Daniel Pauly	Study of the decline of fish stocks and the ecosystems' response to human pressure.	France
2009	Paul R. Ehrlich	Population and human over-population.	USA
2010	Simon A. Levin	Mathematical modeling and empirical studies on the understanding of macroscopic patterns of ecosystems and biological diversities.	USA
2011	Juan Carlos Castilla	Marine ecology, mostly rocky ecosystems and their sustainability.	Chile
2012	Daniel Simberloff	Invasive species and their impact in the loss of diversity.	USA
2013	Sallie W. Chisholm	Biological oceanography and marine ecology, mostly for the studies in the understanding of the dominant photosynthetic organisms in the ocean and the microbiology of the oceans from a revolutionary new perspective.	USA
2014	David Tilman	Ecosystem functioning, biodiversity and protection of endangered species.	USA