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REVIEW

Long-Term Studies of Vegetation Dynamics

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By integrating a wide range of experimental, comparative, and theoretical approaches, ecologists are starting to gain a detailed understanding of the long-term dynamics of vegetation. We explore how patterns of variation in demographic traits among species have provided insight into the processes that structure plant communities. We find a common set of mechanisms, derived from ecological and evolutionary principles, that underlie the main forces shaping systems as diverse as annual plant communities and tropical forests. Trait variation between species maintains diversity and has important implications for ecosystem processes. Hence, greater understanding of how Earth's vegetation functions will likely require integration of ecosystem science with ideas from plant evolutionary, population, and community ecology.

The past decade has seen the emergence of a new synthesis in plant ecology that draws together a variety of once disparate approaches in studies of vegetation dynamics. Questions about the determinants of plant life histories, species composition, diversity, productivity, and stability—previously considered separate areas of inquiry—have become increasingly closely integrated. Findings from long-term experimental and observational studies, combined with comparative and theoretical work, have helped synthesize the questions and approaches of evolutionary ecology, population ecology, and ecosystem ecology. The link has come from the realization that many of the same environmental constraints and organismal tradeoffs that shape the evolution of plant morphologies, life histories, and physiologies also influence the dynamics of interspecific interactions and the mechanisms of coexistence that control community and ecosystem functioning (*1–3*). We provide a brief tour of the developments in vegetation science, highlighting areas where known patterns of variation in demographic rates between species have provided insights into the structure, dynamics, and functioning of plant communities.

Successional Dynamics

Successional dynamics are highly predictable and have been described in numerous systems (*4–8*). Early-successional plant species typically have a series of correlated traits, including high fecundity, long dispersal, rapid growth when resources are abundant, and slow growth and low survivorship when resources are scarce. Late-successional species usually have the opposite traits, including relatively low fecundity, short dispersal, slow growth, and an ability to grow, survive, and compete under resource-poor conditions (*5, 6*). These attributes define MacArthur's classical r- and K-selection continuum (*9*) and underpin most explanations of secondary successional diversity.

In the absence of disturbance, late-successional species eventually competitively exclude early-successional species, because they reduce resources beneath the levels required by the early-successional species. Early-successional species persist as a result of two processes. High fecundity and long dispersal allow these species to colonize recently disturbed sites before the dominant competitors arrive. In addition, rapid growth under resource-rich conditions allows them temporarily to outperform late-successional species, even if both arrive simultaneously in a recently disturbed site. We refer to the first mechanism as the competition-colonization tradeoff (*10*) and the second as the successional niche (*11*).

Given that colonist species persist in recently disturbed sites, it is not surprising that they have morphologies and allocation strategies that maximize resource capture in conditions of high light and nutrients. This means that both competition-colonization and the successional niche mechanism operate in parallel in many systems. These two mechanisms are undoubtedly important in many secondary successions, although their roles in maintaining diversity within stable communities are less clear. However, we suspect that in productive habitats, where disturbances are of small spatial extent, the niche mechanism will be more important than competition-colonization. This is because the competitive dominants are abundant and are therefore likely to colonize virtually all disturbances.

The Dynamics of Annual Plant Communities, Grasslands, and Prairies

Understanding of the processes that structure communities of annual and short-lived perennial plants has developed rapidly in the past decade. Progress has resulted from a move away from viewing species in isolation, where details of the ecology are seen as paramount, to a synthetic approach emphasizing the role of tradeoffs (*12–16*). One pivotal character in this new synthesis is seed size. This character has a profound effect on fecundity, establishment success, seedling survival, seedling growth rate, competitive ability, and persistence in the seed bank. Within floras and local communities, seed size generally follows a log-normal distribution, with many small seeded species and few large seeded ones (*16, 17*). The underlying processes driving this pattern are not well understood, but its widespread existence suggests that many plant species are colonization-limited, in agreement with experimental evidence (*18*), and so smaller seed sizes—resulting in increased fecundity and hence improved colonization ability—have a selective advantage.

Seed size is linked with fecundity via the seed size–number tradeoff: For a plant species with constant reproductive allocation, fecundity is inversely proportional to seed size. This unbreakable constraint means that small changes in seed size result in large changes in fecundity, whereas small changes in reproductive allocation have less effect. The magnitude of the variation in per capita fecundity within communities is enormous.

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In Jakobsson and Eriksson's study of 72 grassland species, for example, average per capita seed production varied from 8 to 5711 seeds per plant across a range of life histories (*16*). These differences in per capita seed production were inversely related to seed size, as expected. The advantages of producing large seeds come through increased seedling establishment success and competitive ability (*13, 15, 16, 19*). These two observations lead to a competition-colonization tradeoff, where small-seeded species are good colonists (because of their high seed production) but poor competitors (because of their small seed reserves). In contrast, large-seeded species are good competitors but poor colonists. Combining this idea with the analysis of a 10-year spatially structured data set led Rees *et al.* (*14*) to conjecture that the competition-colonization tradeoff could be an important mechanism maintaining diversity in annual plant communities.

Given its links with so many demographic parameters, it is not surprising that seed size has also been linked with patterns of relative abundance in several communities. Guo *et al.*, analyzing 18 years of census data from permanent quadrats, found a negative relation between seed size and abundance (*20*), as have other short-term studies (*15, 19, 21, 22*), although this is not always the case (*23, 24*). The relations are typically triangular in form, with large-seeded species having low abundance while small-seeded species show a wide range of abundances. The inverse relation between fecundity and seed size undoubtedly plays an important role in determining this pattern. However, several other processes also linked with seed size are thought to be important. For example, small-seeded species often have long-lived seeds (*25*) and often suffer lower rates of predation (*26, 27*). In addition, small-seeded species often produce small plants, and so a greater number may be packed into a given area (*28*).

In desert annual communities, most species have long-lived seeds, and this is thought to allow coexistence via the storage effect (*29*). Using a combination of long-term observational studies (10 years), experiments, and theoretical modeling, Venable and colleagues have shown that small-seeded species have much higher variation in fecundity from year to year than do large-seeded species, and this selects for increased dormancy and efficient predictive germination (*12, 30, 31*). This pattern of life-history variation is consistent with the theory that dormancy and large seed size are partially substitutable bet-hedging strategies (*32*). Predictive germination allows smaller-seeded species to have greater germination in years of higher reproductive success, and to limit their losses when conditions are unfavorable. Larger-seeded plants buffer population dynamics because greater parental nutrient supply allows seedlings to establish under less favorable conditions, but this comes at a cost, because fewer seeds can be produced when conditions are more favorable. For coexistence to occur via the storage effect, shifts in competitive ability between years and species-specific germination responses to temporal variation are required. Both of these conditions appear to be met (*30, 31*), which suggests that coexistence is promoted via the storage effect, because long-lived seeds allow species to exploit different temporal niches.

Against this elegant backdrop of tradeoffs, there is considerable variance about the estimated relations. For example, Jakobsson and Eriksson could attribute only ~40% of the variation in per capita seed production to seed and plant size (*16*). Much of the unaccounted 60% of the variation is undoubtedly related to interspecific niche differences in seasonal phenology, allocation strategies, resource requirements, and plant architecture, to name a few possibilities. The importance of niche differences in maintaining diversity has been implicated in many studies. For example, Turnbull *et al.* tested the predictions of the competition-colonization hypothesis using a guild of annual plants (*13*). In an experiment where seeds of eight species were added to quadrats in equal numbers, the large-seeded species were found to dominate the community when sowing density was high. This is consistent with the idea that large seed size confers a competitive advantage, as assumed by the competition-colonization model. However, even at the highest sowing density, where colonization limitation of the dominant competitors was removed, the inferior competitors were not excluded from the system, suggesting the presence of species-specific niches (*13*). The niche dimensions thought to be important in this system are growth rate, seasonal phenology, and rooting depth.

Similar niche dimensions are important in the perennial prairie grasslands of North America (*33*). Addition of seed of 54 grassland perennial species to native prairie plots led to a sustained 80% increase in plant species richness over a 4-year period (*34*). Plots with greater initial species richness were invaded by fewer of the added species. Invader success also depended on the initial abundances of plant functional groups in the plots, but in this case, successful establishment was independent of seed size. This suggests that local biotic interactions and recruitment dynamics jointly determined the diversity and composition of these low-nitrogen prairie communities (*34*).

Recent theoretical studies on spatially structured competitive systems have highlighted the potential importance of short-range dispersal in allowing coexistence (*35*). Unlike the competition-colonization hypothesis, where competitively inferior species must produce more seeds or disperse them further, this work has demonstrated the importance of rapid exploitation strategies. An exploiter species has local dispersal, fast growth, early maturation, and small adult size. These traits allow an inferior competitor to exploit gaps in the vegetation efficiently. This pattern of trait variation appears to occur in many annual communities where small-seeded species produce small plants, achieve high densities, and have rapid growth rates, but exhibit no obvious morphological features for dispersal. It also occurs in perennial grasslands, where some species have high growth rates and high allocation to vegetative spread via rhizomes. This complex pattern of traits is clearly related to the successional niche, where dominance of the early-successional species in recently disturbed sites depends on rapid growth. The role of exploitation strategies in communities of long-lived plants is currently an open question.

A corollary of the competition-colonization tradeoff is that recruitment of the competitively dominant plant species should be seed-limited (*36*). This, in turn, means that herbivores that reduce seed production are more likely to reduce the population density of dominant competitors than that of subordinate competitors. Results from long-term experiments involving seed addition and 10-year herbivore exclusion in mesic grassland in southeast England do not support these predictions. On the contrary, seed limitation was commoner among the nondominants than expected, and no evidence of seed limitation among the dominants was found; these results strongly suggest that a competition-colonization tradeoff cannot promote diversity in this system (*37*), although it is consistent with the successional niche hypothesis. However, one finding was consistent with the competition-colonization tradeoff: Where seed limitation was demonstrated, it was correlated with seed size. In a guild of 20 fugitive herb species, only three proved to be seed-limited, but these were the species with the three largest seed sizes. The insect herbivores that reduce seed production in these three species are likely, therefore, to depress average plant population density.

The general effect of herbivores on plant species richness is thought to be positive, but there are counterexamples (*38*). Much of the theory of plant-herbivore dynamics rests on the existence of a tradeoff between palatability and competitive ability (*39*). Plant species that grow fastest in the absence of herbivory are assumed to do so because they invest in growth rather than defense (*40*). These palatable species are predicted to reduce diversity when herbivores are absent by outcompeting the more slow-growing species (*41*). In such a system, selective feeding by herbivores could change the identity of the dominant plant (e.g., an unpalatable species replaces the palatable species), but on its own, selective herbivory cannot promote plant species richness. To do this, herbivory must act in a frequency-dependent or densitydependent manner, so that the palatable species gains some form of rare-species advantage and is not competitively excluded by the ungrazed plant (*42*). There is a growing literature on the indirect effects of herbivores on community dynamics as mediated by altered rates and patterns of nutrient cycling (*43–45*). The roles of pathogens (*46*) and mycorrhizae (*47*) in vegetation dynamics are also attracting increasing attention.

Temperate and Tropical Forest Communities

Many studies in vegetation dynamics have focused on annuals and short-lived perennials, because it was thought that trees were so long-lived that there was no prospect of obtaining important insights into the community dynamics of forests. Advances in theoretical modeling linked to long-term, painstaking monitoring of mortality and recruitment in forest plots have revolutionized the field (*48–50*). In addition to this work, the existence of a detailed fossil record allows us to explore questions concerning the historical determinants of species richness.

The extent of tree diversity varies considerably according to region. There are tens of coexisting canopy species in a typical stand in North America or Europe, whereas there are hundreds in a typical stand in the tropics. Explanations of this pattern fall into two groups. Species-packing hypotheses posit that diversity is constrained at lower levels in the temperate zone than in the tropics, and that diversity is near the upper feasible bound in all places. In contrast, macroevolutionary hypotheses contend that diversity is constrained solely by the regional balance between speciation and extinction rates. Thus, temperate-zone diversity is well beneath the theoretical limits to species packing because extinction rates are higher in the temperate zone than in the tropics, or speciation rates are lower, or both.

Temperate forest trees provide a unique example in which compelling evidence points to the macroevolutionary explanations. Pleistocene glaciation was most severe in Europe (where advancing glaciers pushed temperate trees against the Alps), intermediate in North America, and least severe in east Asia (*51*). Tree diversity is currently highest in temperate east Asia, intermediate in North America, and lowest in Europe (e.g., 729 species in 177 genera in temperate east Asia, 253 species in 90 genera in eastern North America, 68 species in 37 genera in western North America, and 124 species in 43 genera in Europe). Moreover, the pattern of diversity appears to be one of differential removal of species from an initially similar pre-Pleistocene flora. The fossil record of trees is remarkably good in all regions and supports this interpretation. For example, only 29% of the 180 fossil genera in Europe survived from the mid-Tertiary to the present, versus 47% of the 75 fossil genera in western North America, 82% of the 60 fossil genera in eastern North America, and 96% of the 122 fossil genera in northern and east-central Asia (*51*). This pattern of differential extinction explains most, but not all, of the current diversity gradient from Asia to Europe. Additional evidence implicates higher supply rates of species in Asia relative to North America, caused by the proximity and connectivity of temperate and tropical forests (*51*). Both explanations imply that temperate forest diversity, at least in North America and Europe, is well beneath the theoretical limits to species packing.

Recent long-term studies point to two factors that are important worldwide in maintaining diversity in forests: gap-phase succession and microhabitat specialization. Gap-phase succession is ubiquitous in forests and underpins most explanations of successional diversity (*4*, *6*). The successional niche mechanism is the dominant factor in mesic habitats with low fire frequency, because colonizing propagules of late-successional species are usually already present when gaps form (*11*, *52*, *53*). In xeric habitats with stand-destroying fires, the competition-colonization mechanism may be dominant (*54*). Compared to late-successional species, early-successional species tend to have long-dispersal, low-density wood, which leads to rapid growth in height, short longevity, early maturation, short-lived leaves, low specific leaf area (ratio of leaf mass to surface area), high rates of mortality under resource deprivation, and low total leaf area per unit mass (*50*, *55–57*) (Fig. 1). Mechanistic models of several temperate forests explain how these attributes contribute to successional diversity and are routinely used as management tools

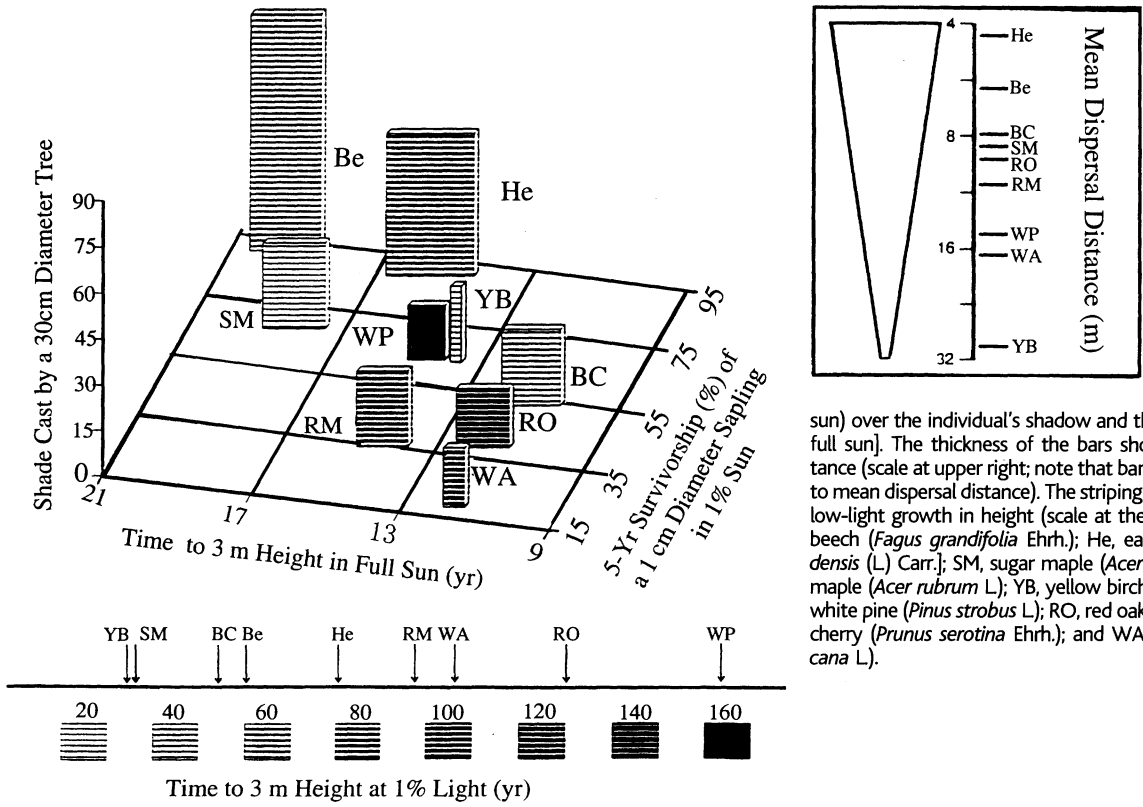

Fig. 1. Tradeoffs among tree species in a forest in the northeastern United States. The horizontal axes show high-light growth in height (time from seedling to 3 m in height) and low-light survivorship (5-year survivorship for a sapling 1 cm in diameter). The vertical axis gives the amount of shade cast by an individual tree [difference between the spatial integral of ln (% of full sun) over the individual's shadow and the corresponding integral for full sun]. The thickness of the bars shows the mean dispersal distance (scale at upper right; note that bar thickness is inversely related to mean dispersal distance). The striping pattern on the bars gives the low-light growth in height (scale at the bottom). Abbreviations: Be, beech (*Fagus grandifolia* Ehrh.); He, eastern hemlock [*Tsuga canadensis* (L) Carr.]; SM, sugar maple (*Acer saccharum* Marsh.); RM, red maple (*Acer rubrum* L); YB, yellow birch (*Betula alleghaniensis*); WP, white pine (*Pinus strobus* L); RO, red oak (*Quercus rubra* L); BC, black cherry (*Prunus serotina* Ehrh.); and WA, white ash (*Fraxinus americana* L).

(*50*). A number of studies suggest the existence of additional tradeoffs among plant attributes that may also affect successional diversity (*6, 25, 50, 57*).

Each successional strategy persists by specializing in a particular part of the endogenous heterogeneity created by single tree deaths and larger disturbances. Tree species also coexist by specializing in exogenous heterogeneity created by spatially variable topography, climate, and the geological parent material of soils. The descriptive study of associations among tree species and attributes of the physical environment has a long history in ecology, and is now beginning to gain a quantitative and mechanistic foundation (*58–60*). The problem of exogenous heterogeneity is more difficult than the successional problem, not only because it requires the study of several linked locations, but also because successional diversity is always present and must be separated from the effects of the heterogeneous physical environment.

Nonetheless, studies to date indicate that habitat specialization, particularly in response to differential water availability, is an important mechanism at large spatial scales (*58*). One surprise is that spatial variation in soil fertility is caused by tree species composition as well as by purely physical processes. Nitrogen is the primary limiting nutrient in temperate forests, and the rate of nitrogen mineralization depends strongly on the lignin-to-nitrogen ratio of leaf litter (*61*). Species differ in lignin-to-nitrogen ratio, causing the nitrogen availability to vary from tree to tree by more than a factor of 2 (*62*). These differences in litter chemistry are not obviously related to successional status or shade or drought tolerance, and the implications of litter feedbacks for the regulation of species composition are not well understood.

Life-history tradeoffs and the coexistence of species are also central themes in tropical forest ecology. But assembling demographic data from such diverse forests has been a challenge. Only a few long-term studies have been able to examine life-history variation in a large number of species from a single community. The paradigm of life-history variation has led tropical biologists to examine correlations among demographic traits: Shade tolerance correlates with slow growth, high survival, large seed size, and relatively low fecundity, whereas the ability to colonize disturbed sites associates with fast growth, low survival, and many small seeds (*63–68*). Rapid growth and high fecundity allow pioneer species to colonize canopy openings quickly, but the cost is poorly defended leaves and wood (*65, 69*), so mortality is high. At the opposite extreme are species that invest in well-protected leaves, wood, or roots, allowing persistence for many decades as saplings, but the cost is slower growth and larger seeds that are poorly dispersed. These tradeoffs fit the successional niche theory (*11*), which states that pioneers outgrow shade-tolerant species in high light but cannot survive in low light (*65, 70*). The competition-colonization tradeoff (*10*), although present, is probably not important, because shade-tolerant species as a group are abundant and readily colonize small disturbances such as treefall gaps (*71*). Individual species of shade-tolerant trees, however, are highly dispersal-limited (*72–74*), so the argument (*75*) that large-scale loss of habitat could lead to extinction is relevant to individual species of shade-tolerant trees.

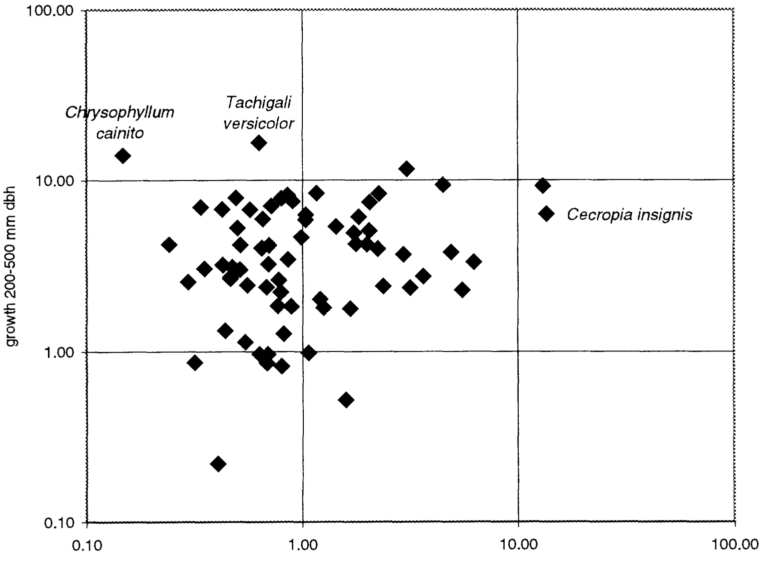

Fig. 2. Growth at juvenile size versus growth at adult size in tree species at Barro Colorado Island, Panama, on a log-log scale (dbh, diameter at breast height). The generally positive trend suggests that life history (as reflected by growth) is consistent through development; however, the relation is weak and triangular in form. Many species have very low growth rate as juveniles but high growth rate as adults. Species such as *Chrysophyllum cainito* and *Tachigali versicolor* shift life history as they develop. [Redrawn from data in (*76*)]

Whether the single axis from colonizer to shade-tolerant species adequately describes life-history variation in tropical trees has been a subject of debate. For instance, intensive studies of entire communities in Panama and Malaysia showed that the association among colonizing ability, high growth, and low survival holds in saplings but gradually breaks down in larger trees: Species that are shade-tolerant and slow-growing when small can be either fast-growing or slow-growing as adults (*66, 76*) (Fig. 2). Long-term work on a small set of species has similarly documented developmental shifts in life-history strategy (*77, 78*). Thus, descriptions of demographic patterns and tradeoffs within sites have produced a solid body of theory on life-history variation. The next step is to show whether this variation accounts for coexistence of species and can predict broad patterns of forest diversity and structure.

A second major paradigm of tropical tree biology is the Janzen-Connell hypothesis, namely, that seeds or seedlings close to a conspecific individual will suffer higher mortality from specialist herbivores or pathogens than those that are more widely dispersed (*79, 80*). The distance and density dependence inherent in this hypothesis generates a rare-species advantage that can maintain unlimited species diversity. Most important, when trying to explain diversity in tropical forests, is the fact that the effect becomes stronger as species diversity increases. The assumptions of the hypothesis appear to be true in many systems, resulting in characteristic dispersion patterns (*66, 81–84*), but it remains to be seen whether it can explain diversity or species composition. A limitation of the current paradigm—both theory and observation—is that it invokes no intrinsic species differences. This can lead to high diversity, but it begs the question of why some species are abundant and others rare. An extension of the hypothesis would be that species vary in their ability to tolerate high density, and perhaps that this variation correlates with the life-history axis.

With 1000 species growing together in a tropical forest, it is difficult to imagine that life history or habitat differences could be found for every one, which lends credence to the Janzen-Connell hypothesis. Some species are likely to be functionally similar, and thus to have dynamics driven by ecological drift (*85*). The challenge is to determine whether (and, if so, when) drift has more of an effect than species differences and tradeoffs, and which aspects of community structure are predicted by tradeoffs versus drift. Life-history theory has made a contribution: Pioneer species are rare, and the mixture of life-history guilds clearly structures forests. It remains to be seen whether Janzen-Connell effects explain differences in abundance.

Ecosystem Consequences of Interspecific Variation in Demographic Traits

What are the consequences of this diversity of plant traits for ecosystem processes? A long-term study of the dynamics of grasslands suggests that greater diversity may lead to greater stability of total community biomass but may simultaneously destabilize abundances of individual species (*86, 87*). Although there are a large number of alternative explanations for the patterns observed [e.g., (*88*)], this research has sparked a theoretical re-exploration of diversity-stability-productivity relations. This work has built on the classical work of May (*89*) and has used more recent tradeoff-based models of multispecies competition and coexistence via habitat heterogeneity (*90*). It has shown that the stabilizing effects of diversity on total community attributes can come, in part, from statistical averaging effects (*91*). Stability is also conferred by the ability of one species to increase and, at least partially, take the place of a competitor that has been harmed by some perturbation. In both cases, diversity has such effects only if species differ in their traits, indicating that the most important relevant measure of diversity is the among-species variance in functional attributes (*90*).

A variety of experimental studies of grassland communities, both in short-term growth chamber or greenhouse settings (*92, 93*) and in longer term field experiments (*94–96*), have shown that greater plant diversity is associated with greater community productivity. A large number of alternative hypotheses have been proposed as explanations for such patterns [e.g., (*88, 90, 92–95, 97–101*)]. Some of these use models of coexistence based on tradeoffs in species abilities to exploit limiting resources, and they predict that greater diversity should lead to greater community productivity [e.g., (*90*)]. This would occur because greater diversity increases the range of ways that species exploit limiting resources, leading to more complete use of the limiting resources.

The relation between plant productivity and herbivore impact is the subject of an unresolved debate (*102*). There is a school of thought that this relation is a fundamental ecosystem property (*103*); others argue that the patterns are weak and equivocal. Herbivore impact is argued to be low in unproductive systems because these can support only very low herbivore densities, and the plant traits associated with low productivity also serve to make the plants unpalatable to herbivores (e.g., small, long-lived leaves, low in nitrogen and high in secondary compounds). At high plant productivity, herbivore impact is minimal, because herbivore productivity is so high that natural enemy populations are able to maintain herbivore populations at low densities. Only at intermediate productivities are herbivores common enough to reduce total plant biomass (herbivore numbers peak here because productivity is too low to support influential natural enemy populations). The evidence for this is reasonably strong in tundra ecosystems (*103*), and recent experimental work using microorganisms in chemostats (*104*) suggests that it might be of more general importance.

For a given level of primary productivity, variations in trophic structure can have striking effects on plant community structure. The evidence for this is very strong in freshwater lakes, where the trophic components are phytoplankton, zooplankton, planktivorous fish, and top carnivorous fishes (*105*). This simplicity is not seen in terrestrial plant communities where the primary producers are large and often very long-lived plants (*102*). Nevertheless, there are several examples of keystone herbivores in terrestrial systems [e.g., seed-feeding rodents in desert grasslands (*106*), rabbits in mesic grasslands (*107*), lemmings in arctic tundra (*103*)].

All of this might seem to suggest that causation flows from species traits to species abundances to ecosystem functioning, but other work in grasslands shows that this would be an overly simple perspective. For instance, invasion of a fire-susceptible grass into Hawaii led to greatly increased fire frequency, which then led to the loss of much of the native flora that was fire-sensitive (*108*). Similarly, invasion of an N-fixing shrub into Hawaii led to major increases in soil N availability, which then favored invasion by other exotic plant species that had high N requirements (*109*). In Minnesota grasslands, decreased densities of a mammalian browser (deer) led to large increases in an otherwise rare legume, which had fixed sufficient N after a decade to double soil fertility and grassland productivity (*110*).

Conclusions

Long-term work in vegetation dynamics has shown the potential insights that can come from studying the mechanisms of interspecific interaction in the context of the tradeoffs that organisms face in dealing with the constraints imposed by their habitats (*1–6*). There is increasing evidence that these tradeoffs influence the general patterns of succession and the maintenance of diversity within communities. The consistency of the successional patterns observed across widely different ecosystems demonstrates that strong deterministic processes are at work. However, within mature communities, species may be more similar in their traits, making the forces that operate weaker and leading to slower dynamics after perturbation. If a wide range of guilds within these communities have slow dynamics (and hence approximate neutrality), it will be difficult to assess the predictive ability of neutral models, such as those developed by Hubbell (*111*).

The focus on patterns of life-history variation that naturally arise through allocation constraints or through evolutionary considerations is leading to a predictive theory of vegetation dynamics. Further insights into vegetation dynamics are likely to come from an expanded synthesis of evolution, population, community, and ecosystem ecology; from additional comparative, observational, and experimental studies; and from theory that links these together.

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VIEWPOINT

Investigating Long-Term Ecological Variability Using the Global Population Dynamics Database

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The Global Population Dynamics Database (GPDD) is an important new source of information for ecologists, resource managers, and environmental scientists interested in the dynamics of natural populations. It comprises more than 4500 time series of population abundance for over 1800 animal species across many taxonomic groups and geographical locations. The GPDD offers great potential for asking comparative questions about the nature of population variability. We illustrate this by characterizing some critical features of ecological variability, variance growth, and spectral reddening.

The gathering of population time series is a lengthy process, and many ecologists have committed themselves to a lifetime of work to accumulate detailed information on populations at certain sites over many years. This information has often been difficult for these people to publicize and for others to obtain. This in turn has hampered the formulation and testing of general ecological theories and the investigation of large-scale spatial and temporal patterns. The goal of the Global Population Dynamics Database (GPDD) has been to use the potential of the global Internet to address this challenge and make available to ecologists an extensive database of ecological time series. The GPDD (*1*) (Fig. 1) was built by the NERC Centre for Population Biology (Imperial College, Silwood Park, United Kingdom) in collaboration with the National Center for Ecological Analysis and Synthesis (University of California, Santa Barbara), and the Department of Ecology and Evolution, University of Tennessee. Comprising more than 4500 time series of population abundance longer than 10 years for over 1800 animal species across many geographical locations, it is the largest collection of animal population data available to ecologists. The GPDD is constantly updated with new information from the published literature and from previously unpublished data, and its freely searchable structure offers a wealth of opportunities for comparative analyses of population dynamics. We illustrate this potential [see also (*2*)] by investigating the so-called "more time, more variation" effect (*3*, *4*) in animal populations using the GPDD.

Preliminary studies have shown that the magnitude of temporal variability depends on a species' body size, its reproductive rate, and the features of the food web structure in which the species is embedded (*5*). However, there is also a prevailing tendency, across a wide variety of species, for temporal variability to increase with the length of the census (*3*, *5*–*9*). This "more time, more variation" effect has already inspired considerable discussion, both as to its possible origin (*3*, *4*, *10*–*12*) and implications (*3*–*7*, *10*). It has usually been associated with "spectral reddening" (a tendency for low or high abundances to be followed by more of the same) of population

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