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Plant Biodiversity Change Across Scales During the Anthropocene

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biodiversity, climate change, habitat fragmentation, land use, nitrogen deposition, scale

Abstract

Plant communities have undergone dramatic changes in recent centuries, although not all such changes fit with the dominant biodiversity–crisis narrative used to describe them. At the global scale, future declines in plant species diversity are highly likely given habitat conversion in the tropics, although few extinctions have been documented for the Anthropocene to date (<0.1%). Nonnative species introductions have greatly increased plant species richness in many regions of the world at the same time that they have led to the creation of new hybrid polyploid species by bringing previously isolated congeners into close contact. At the local scale, conversion of primary vegetation to agriculture has decreased plant diversity, whereas other drivers of change—e.g., climate warming, habitat fragmentation, and nitrogen deposition—have highly context-dependent effects, resulting in a distribution of temporal trends with a mean close to zero. These results prompt a reassessment of how conservation goals are defined and justified.

Contents

INTRODUCTION	564
WHAT IS BIODIVERSITY AND WHY DO WE CARE ABOUT IT?	565
Definitions and Metrics of Biodiversity	565
Why People Care About Biodiversity	566
METHODS OF STUDYING TEMPORAL BIODIVERSITY CHANGE	566
SPATIAL AND TEMPORAL SCALES	567
THE GLOBAL SCALE	567
Anthropocene Extinction	568
Anthropocene Speciation	569
Global-Scale Conclusions	569
THE REGIONAL SCALE	569
Observed Species Richness Changes at the Regional Scale	570
Functional and Phylogenetic Diversity	571
Underlying Causes and the Future of Regional-Scale Plant Diversity	571
Regional-Scale Conclusions	572
THE LOCAL SCALE	572
Temporal Plant Biodiversity Trends in Resurvey Studies	572
Effects of Land Use	573
Effects of Habitat Fragmentation	574
Effects of Climate Warming	575
Effects of Nitrogen Input	576
Local-Scale Conclusions	577
PLANT BIODIVERSITY CHANGE ACROSS SCALES	577
IMPLICATIONS FOR CONSERVATION	578
FROM CURRENT KNOWLEDGE TO FUTURE RESEARCH	580

Anthropocene:

the time period of especially profound human impacts on the earth, starting 300–500 years ago (note that other definitions exist)

Nonnative species:

species present in a given region because they were introduced there by people

Native species:

species present in a given region without having been introduced there by people

INTRODUCTION

Over the past 30 years, ecology, evolution, and conservation biology have coalesced around the concept of biodiversity. At the same time, driven by the sense of a current or pending crisis, innumerable international agreements, national policies, and research organizations have adopted biodiversity as their central focus. There is thus tremendous interest among scientists, policy makers, land managers, and the general public in understanding patterns and causes of biodiversity across space and time. This interest stems both from a desire to conserve biodiversity as an end in itself and from the potential for biodiversity changes to have an impact on the benefits people derive from nature, such as food, fiber, and clean air and water (66).

Human domination of the biosphere in recent centuries—a period of time often referred to as the Anthropocene (96)—is widely considered to have elevated species' extinction rates to the point of a global-scale biodiversity crisis (6, 70). However, for plants, extinction-rate estimates are highly uncertain, and human activities, such as species introductions that bring close relatives into geographic proximity, may have actually increased the rate of plant speciation (103). At subglobal scales of observation—from local study plots of a few square meters to entire continents—recent research points to immense variability in temporal biodiversity trends (24, 69, 87, 111). For example, nonnative species have caused declines in some native species at the same time that they

have greatly enriched regional floras (87, 124). By understanding how and why plant biodiversity has changed in recent centuries, we can improve predictions of how it will change in the future.

A huge literature concerns patterns of plant species diversity and the factors that influence these patterns over space and time. Studies range from those addressing how factors such as productivity or land use influence diversity at small spatial scales (69, 117) to those addressing the effects of nonnative species on regional-scale diversity (87, 124) and the quantification of global extinction and speciation rates (45, 78, 103). Here, we review this literature and present a synthesis of knowledge of patterns and causes of plant biodiversity change during the Anthropocene across spatial scales.

Our review integrates multiple lines of evidence. First, at each spatial scale—global, regional, and local—we describe observed or estimated temporal trends of plant diversity in nature, which ultimately represent the phenomena in need of explanation. Second, at regional and local scales, we assess spatial correlations between plant diversity and potential causal factors (e.g., land use or climate), which provide the basis for making space-for-time predictions. If, for example, sites with higher temperature harbor greater plant diversity, warming might be expected to cause an increase in plant diversity over time (94). Third, when possible, we evaluate manipulative experiments in which the response of plant diversity to particular factors (e.g., temperature increase) was quantified. In addition to drawing on many individual case studies, we draw on the rich body of existing reviews and meta-analyses on particular drivers of biodiversity change. We begin by briefly reviewing some basic concepts in the characterization and study of biodiversity.

Space-for-time prediction:

a prediction for the effect of a variable over time based on how the response correlates to this variable spatially

WHAT IS BIODIVERSITY AND WHY DO WE CARE ABOUT IT?

Definitions and Metrics of Biodiversity

The term biodiversity means many things to many people. By its broadest definition, biodiversity is synonymous with all life on earth, but this definition is scientifically unusable. Here, we adopt the scientifically operational definition of biodiversity as the variety of organisms found in a given place and time, and we focus this review more narrowly on species diversity: any measure of variety that begins by determining the taxonomic identity of each organism in a community. The vast majority of studies documenting spatial and temporal patterns of biodiversity concern species diversity, with by far the most common metric of diversity being species richness—the number of species found in a given place and time. Most of the studies on which this review is based are about species richness.

In some instances, we also draw on studies using one of the many indices that incorporate data on species' relative abundances, traits, or phylogenetic relationships (62). Indices of species diversity incorporating abundance data (e.g., the commonly used Shannon and Simpson indices) aim to capture differences in the evenness of abundances: A community with two species at equal abundance is considered more diverse than a community in which one of the two species is far more abundant than the other. Indices of functional and phylogenetic diversity capture the variety of trait values represented by species in the community and the amount of evolutionary history (i.e., portion of the tree of life) those species represent, respectively (51, 112). For both functional diversity (e.g., based on leaf traits) and phylogenetic diversity, a community of conifers and angiosperms is typically more diverse than a community of only conifers or of only angiosperms. At present, studies have been too few and too heterogeneous to permit generalizations about functional or phylogenetic diversity, but we note selected cases where these measures appear to behave differently than species richness.

Ecosystem services: benefits that people derive from ecosystems, such as food, fiber, and clean water

Why People Care About Biodiversity

Patterns of biodiversity across space and time are among the most striking features of nature, and they beg for scientific explanation. Why are there so many more plant species in the tropics than in temperate and polar regions? How do dozens or even hundreds of plant species coexist in small areas despite similar requirements for a small number of resources? These questions and many others motivate scientists to care about biodiversity as a fundamental property of the natural world.

When we hear the word biodiversity, the word conservation is rarely far behind. Many people care deeply about biodiversity for its own sake: We attribute great moral and cultural value to the variety of living organisms. This presents biodiversity scientists with the considerable challenge of separating our deep passion for biodiversity conservation from the need for an impartial approach to credible science (68, 101). We have tried to make this separation, presenting and interpreting the data as they appear in the literature and returning to conservation questions during the discussion.

People also care about biodiversity because of its potential to provide ecosystem services that benefit human well-being (13). By the broad definition of biodiversity as life on earth, this argument is true by definition: People rely on other organisms and ecosystems directly or indirectly for every facet of our lives. By the narrower, scientifically viable definition of biodiversity as variety per se in particular places and times, there is vigorous debate as to whether empirical results on links between biodiversity and ecosystem services provide a general justification for biodiversity conservation (63, 111, 118). We revisit this issue in the discussion.

METHODS OF STUDYING TEMPORAL BIODIVERSITY CHANGE

Various methods can be used to infer patterns and causes of temporal biodiversity change, each of which comes with advantages and disadvantages. First and foremost, we can directly observe changes over time in particular places. Plants stand still, so at the local scale we can count species and estimate abundance with good accuracy. By conducting long-term vegetation monitoring or revisiting plots surveyed in the past, many studies have quantified temporal changes in plant biodiversity at the local scale (e.g., up to hundreds of square meters). However, such studies rarely cover more than ~50 years of time, and they cover only a subset of situations of interest.

In some cases, temporal observational studies provide some scope for inferring causes, via two methods. First, one can test a priori predictions about the direction of long-term trends based on cause-and-effect hypotheses, such as a positive effect of climate warming on alpine species diversity driven by colonization of species from lower elevations (74). Second, one can test for temporal correspondence between fluctuations in diversity and those of a given hypothesized driver of change (e.g., precipitation; 37).

At larger spatial and temporal scales, one can combine data on the extant flora, notes of early explorers, fossils (in some cases), and information on species' biogeographic origins to reconstruct the pre-Anthropocene flora as a basis for characterizing changes through to the present (e.g., 87, 88, 124). An advantage here is the ability to cover the full time period of interest, although historical data include more uncertainty than local-scale observations and are unavailable in many regions.

The environmental correlates of plant biodiversity patterns across space provide insights into possible causes of temporal change. For example, if we assume that an unlogged forest represents the historical state of a logged forest, the difference between the two types of forest is an estimate of the change in plant diversity over time resulting from logging. Similar space-for-time inferences have been applied to many potential drivers of change, such as nitrogen deposition (91, 97) and climate change (94). An advantage of the space-for-time approach is the massive amount of

applicable data. The main limitation is considerable uncertainty in the assumption that temporal change will mirror spatial gradients. Potential confounding variables limit our confidence in the causal inference: For example, people cut down trees in places with particular soil conditions, such that soil differences rather than logging might be the cause of an observed spatial pattern. In addition, reference sites themselves may have undergone major temporal changes (2, 8).

Finally, manipulative experiments provide the most direct means, in principle, of controlling potentially confounding factors, although applying experimental results to nature is difficult. For example, variables such as temperature or anthropogenic nutrient input change gradually in nature but are typically changed instantaneously in experiments, with potentially important consequences (47, 93, 125), such as limited opportunities for colonization by new species that might offset rapid declines of residents. The magnitude of experimentally imposed environmental change also often greatly exceeds the change observed or expected in nature (7).

SPATIAL AND TEMPORAL SCALES

Patterns of biodiversity frequently depend on the spatial and temporal scales of observations. Although it is possible for patterns and processes to interact across scales (e.g., local diversity can depend on regional diversity; 83, 110), changes in species diversity are not necessarily correlated across scales (65). For example, nonnative species introductions across continents can cause large increases in regional species richness at the same time that extinctions cause a global decrease.

We recognize three spatial scales in this review. The global scale includes the entirety of the planet. The local scale refers to study plots used in field-based studies—typically 1–1,000 m². The regional scale is almost anything between local and global but most often refers to areas of thousands of square kilometers, such as most countries, states, or provinces. One could add additional levels (e.g., the landscape scale between local and regional), but most studies fall cleanly into one of these categories.

Plant biodiversity can fluctuate up and down, so the observed temporal trend in a given place will depend on when and for how long data were collected. Our focus here is the Anthropocene, defined broadly as the era during which humans have had a profound impact on the earth, although considerable debate surrounds the exact timing of the onset (92). Here, we loosely define the Anthropocene as applying to the past 300–500 years.

THE GLOBAL SCALE

Roughly 350,000 plant species on earth have been named, representing an estimated 80–90% of the global total (45, 78). Since the first vascular plants evolved >400 Mya, global plant diversity has increased markedly. Surprisingly, the periodic mass extinctions observed for animals do not appear to apply to plants (120, 122). This is one clue that plants might be comparatively resistant to extinction. Still, plant extinctions have occurred throughout history and can be characterized by background extinction rates, which help to put the Anthropocene in context. That said, using the fossil record and/or molecular phylogenies to generate extinction and speciation estimates is fraught with uncertainties, and all estimates should be interpreted as very rough approximations. In addition, the types of Anthropocene extinction and speciation events we have been able to observe (rare island endemics and hybrid polyploid species during the first decades of their existence, respectively) are exactly of the type not represented in the fossil record (40, 80). Nonetheless, the central tendencies of background plant extinction rates fall mostly in the range 0.05–0.15 species per million species per year (S/MSY) (see **Table 1**), whereas background speciation rates (based on the same data sources) fall mostly in the range of 0.1–1.0 S/MSY (**Table 1**).

Mass extinction: a massive, rapid, and globally widespread episode of extinction

Background extinction rate: the long-term average rate of species extinction in a lineage prior to major human impacts

Hybrid polyploid species: a species created via hybridization between two “parent” species and a subsequent multiplication of chromosome number of their descendants

Table 1 Estimated rates of plant extinction and speciation in the distant past (background), the recent past (Anthropocene), and the future (projected)

Median/mean rate (S/MSY ^a)	Data source(s)	Data type
Extinction: background		
0.05	De Vos et al. (21)	Phylogenetic analysis
0.07 ^b	Levin & Wilson (56)	Species durations in the fossil record
0.13	Stanley (95)	Species durations in the fossil record
Extinction: Anthropocene, to date		
0.98	IUCN Red List (extinct or extinct in the wild) (42)	142 extinctions from 1600 to 2016 ^c
4.1	World Conservation Monitoring Center (127)	592 extinctions from 1600 to 2016
5.2	Regan et al. (81)	33 extinctions out of 16,000 species over 400 years in Australia ^d
Extinction: Anthropocene, conservative projection		
50	Reid (82), van Vuuren et al. (109)	5% extinction rate spread over 1,000 years ^e
Speciation: background		
0.65 ^b	Levin & Wilson (56)	Ages of genera and number of species in each genus
0.14	De Vos et al. (21)	Phylogenetic analysis (net diversification plus extinction)
Speciation: Anthropocene, to date		
6.3	Thomas (103)	6 new species (in a region with ~3,000) from 1700 to 2015 in the United Kingdom
Speciation: Anthropocene, projection		
No estimates available		

^aSpecies per million species per year or, alternatively, species per species per million years; for example, a speciation estimate of 1.0 S/MSY means that for every million species, one new species will arise each year, or, equivalently, each species is likely to give rise to one additional species every million years.

^bWeighted average for herbs, shrubs, and hardwoods, assuming that 45% of species are woody (evenly split between shrubs and hardwoods) and the rest are herbaceous (31).

^cThe calculation here is as follows: (142 species extinct/350,000 total species)/[(2016 – 1600)/10⁶] million years.

^dRough midpoints from a range of possibilities reported by Regan et al. (81).

^eThe low end of projected percentages of species committed to extinction by Reid (82) is 4% by 2040 and 7% by 2050, but we have no estimate of the time course over which these extinctions will occur; here, we consider 1,000 years a conservative guess.

Anthropocene Extinction

Estimates of Anthropocene extinction are usually made by estimating the proportion of species “committed to extinction” within a specified time frame given habitat loss or other anthropogenic factors, such as climate change. Alternatively, one can also estimate the Anthropocene extinction rate based on species whose extinction has already been observed (or inferred). Given the huge discrepancies between observed and projected extinction rates (98), we treat these rates separately, then discuss Anthropocene speciation.

A report by the World Conservation Monitoring Center in the early 1990s listed 592 plant species as having gone extinct either in the wild or completely from the earth since 1600 (127). The current International Union for Conservation of Nature (IUCN) Red List includes 142 extinct plant species (42). The IUCN evaluated 86 taxa from the initial list of 592 and found that 36 had been rediscovered in the wild, 42 remained classified as extinct, 4 lacked sufficient data to make a determination, and 4 were no longer recognized as distinct taxa. The majority of the 142 IUCN-listed species were not included in the World Conservation Monitoring Center’s list

of 592 (127). There is thus massive uncertainty with respect to undocumented extinctions and unknown extant populations of rare species. Nonetheless, if we take 142 and 592 as somewhere in the ballpark of extinctions that have occurred between 1600 and 2016, we get extinction rates of 0.98–4.1 (**Table 1**; see also 81), 1–2 orders of magnitude higher than the background rate.

The future extinction rate in the face of habitat loss and climate change is even more uncertain. Future risks from habitat loss, often referred to as commitment to extinction, are typically calculated using species-area relationships. As the area of habitat (A) declines, the number of species (S) declines in concert, often following (at least approximately) the relationship $S = cA^z$, in which c is a constant and z the slope of $\log S$ versus $\log A$. This approach involves many questionable assumptions, the details of which are beyond the scope of this review. However, even if one takes at face value a prediction such as 7–25% of species being committed to extinction by 2050 (109), it is not possible to calculate an extinction *rate* without an estimate of the time course over which those extinctions will actually happen. A key point for our purposes here is that even if we take a low-end estimate of 5% extinction (82) and assume a 1,000-year period over which these extinctions occur, the estimated extinction rate (50 S/MSY) is upward of 1,000 times the background rate (see **Table 1**). The time course of extinctions may well exceed 1,000 years (23), but other factors, such as climate change, might also push extinction rates even higher (44, 107).

Anthropocene Speciation

Until recently, analyses of Anthropocene biodiversity change have assumed that speciation is a negligible part of the equation. However, human activities during the Anthropocene include some of the key ingredients in the recipe for speciation, such as the establishment of new populations isolated from the species' native range (114). For plants, hybridization plus a change in chromosome number is an especially efficient and historically common route to the rapid creation of new species (10, 126), although hybridization with nonnative species might also represent a threat to some rare native species (55). Many Anthropocene hybrid polyploid plant species have been documented, but we sorely lack a global compilation. Based on data just for Great Britain, Thomas (103) estimated an Anthropocene speciation rate of 6.3 S/MSY, comparable to the Anthropocene extinction rate to date. We do not know whether the future plant speciation rate will be higher or lower. With human-mediated species introductions showing no sign of deceleration (88), we might expect at least maintenance of the current Anthropocene rate of plant speciation.

Global-Scale Conclusions

- Both extinction and speciation rates have likely increased owing to human activities during the Anthropocene.
- We cannot conclude definitively that the number of plant species on earth has decreased or increased since the onset of the Anthropocene.
- Extinctions during the coming centuries have the potential to greatly outnumber speciation events, causing a decline in global plant species richness.

THE REGIONAL SCALE

At the regional and local scales, immigration joins speciation as an important input term in the biodiversity equation. By far the largest contribution to regional-scale Anthropocene immigration comes from deliberate or accidental human-mediated species introductions among continents, with geographic range shifts within continents playing a comparatively minor role. Considerable

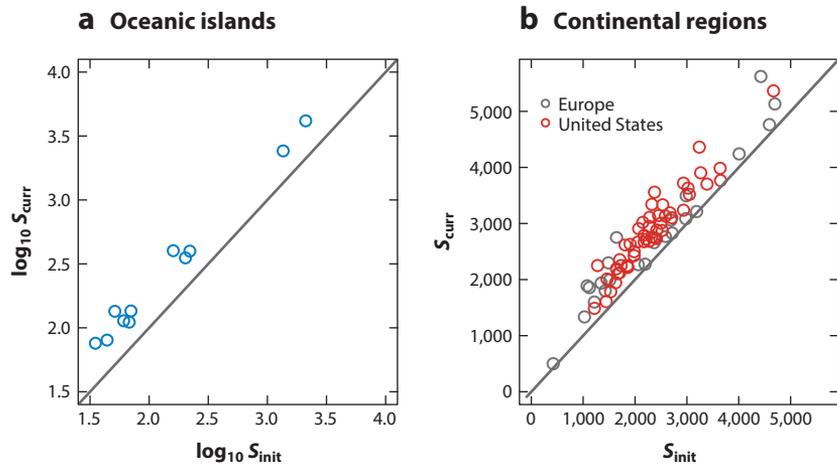


Figure 1

Estimated current species richness (S_{curr}) versus pre-Anthropocene initial species richness (S_{init}) for (a) 11 oceanic islands (data updated from 88) and (b) 23 countries or regions of Europe (data from 124) and the 50 states in the United States [data collated from NatureServe (<http://www.natureserve.org>); see also 87]. Points above the diagonal 1:1 lines show net increases in richness. A log scale was used for the islands for ease of presentation, given the large range in richness among archipelagos.

effort has been invested in documenting nonnative plant establishment across the globe (108). Regional-scale extinctions have been quantified in far fewer regions, although the existing studies provide consistent results on positive net diversity change during the Anthropocene.

Observed Species Richness Changes at the Regional Scale

For 11 islands or archipelagos, largely in the Pacific and Indian Oceans, Sax et al. (89) documented both extinctions and introductions, with the net average effect being a doubling of regional plant species richness during the Anthropocene (see also 88). The sample included the Hawaiian Islands (>15,000 km²) and New Zealand (>250,000 km²), and the proportional increase over time was consistent across archipelagos (see **Figure 1a**). Islands typically experienced <5% extinction and the establishment of roughly as many nonnative species as the original number of native species. The qualitative pattern observed for islands also applies to continental regions of Europe (124) and the United States (87), where the net increase in richness has been roughly 20–25% on average (**Figure 1b**).

With regard to regional-scale changes in plant diversity, the biggest unknown is the number of extinctions in continental tropical regions. In terms of introductions, van Kleunen et al. (108) compiled data on nonnative plant species in 481 mainland and 362 island regions across the globe, including many tropical countries. Continental tropical regions were typically found to be home to dozens to hundreds of nonnative species. In order to gain a rough sense of the proportion of nonnative species in tropical floras, we looked up the total number of plant species in five haphazardly selected African countries (Burundi, Chad, Gabon, Namibia, and Uganda). The proportion of nonnative species varied from 1.4% in Uganda (68/4,900) (67) to 12.2% in Chad (278/2,288) (12), with all five below the average of ~20% in European regions and the United States. At present, it is unknown how these numbers compare with numbers of plant extinctions in the same regions, although upward of 10% extinction (i.e., to match invasions in a country like

Chad) would be quite high even for tropical islands, where species are thought to be particularly prone to extinction (88).

Functional and Phylogenetic Diversity

To our knowledge, Winter et al. (124) performed the only study to address regional-scale changes in plant functional or phylogenetic diversity. At the scale of Europe, phylogenetic diversity (average phylogenetic distance between pairs of species) showed a statistically significant but very small increase: A randomly chosen pair of species is now ~1% more distantly related than it was in the year 1500. Within regions (mostly countries), phylogenetic diversity showed a statistically significant 0.3% decline over the same period. However, it is important to note that a small change in the average phylogenetic distance between pairs of species does not imply a change in total phylogenetic diversity, which was originally quantified in conservation biology as the sum of branch lengths connecting the set of co-occurring species (29). With the addition of so many species, total phylogenetic diversity may well increase even as average pairwise phylogenetic diversity declines, given the tendency for nonnative species to have one or more close relatives in the native flora. This requires caution when interpreting results of phylogenetic or functional diversity metrics designed to statistically control for correlation with species richness (51, 112).

Underlying Causes and the Future of Regional-Scale Plant Diversity

The dominant cause of regional-scale plant diversity changes is clearly the establishment of nonnative species, which in turn depends on both introduction pressure and the suitability of biotic and abiotic conditions (59). Net increases in diversity may be due in part to increased environmental heterogeneity, with a mix of disturbed and undisturbed habitats permitting the persistence of nonnative and native species alike (19, 102). Interestingly, the same economic activities that prompt introductions (agriculture, horticulture, and urbanization) also result in the creation of suitable habitats for many nonnative species and the modification of habitats to the detriment of many native species (38, 79). It is thus difficult to predict future net changes in plant diversity at the regional scale, especially in tropical areas, where increasing international trade and habitat disturbance should promote both nonnative species invasions and native extinctions.

From a theoretical point of view, an elevated rate of immigration via nonnative introductions is expected to increase diversity (84, 110), and for places that have been repeatedly surveyed over time, there is no sign of a recent decline in the rate of new species establishment (88). In general, increasing human activity and anthropogenic habitat modification should accelerate the establishment of nonnative species (57), a process that might be especially important in developing tropical nations. Shifting geographic ranges resulting from climate warming are also expected to bring new species to particular regions (72, 94), and time lags involved in such range shifts create an “immigration credit” for future regional diversity (43).

Much more uncertainty is involved in predicting future extinctions. On the one hand, many species might already be committed to regional extinction, e.g., populations that are on a continual decline, with such populations representing an “extinction debt” (43, 105, 115). The huge number of endemic plant species in tropical biodiversity hot spots, which have experienced massive forest loss, points to the likelihood of a great many regional (and global) extinctions (52). On the other hand, the fact that observed large-scale extinctions to date have been far fewer than predicted (16, 98) and the suggestion from paleobotanical data (120, 122) and more recent extinction data (87) that plants are less extinction prone than other taxonomic groups encourage caution in making predictions of future extinctions.

Immigration credit: species absent from a given region where conditions are suitable and where future introduction is likely

Extinction debt: species in a given region that are on a deterministic path to extinction but have yet to go extinct

Regional-Scale Conclusions

- So far, the number of nonnative plant species established in a given region is typically far greater than the number of species that have gone regionally extinct.
- The resulting net increase in regional richness has been greater on islands than in mainland regions.
- Very little is known about net plant biodiversity changes during the Anthropocene in tropical continental areas, particularly with respect to extinctions.
- Continued regional increases in plant species richness seem likely, but the magnitude is highly uncertain, especially for tropical continental areas.

THE LOCAL SCALE

Our knowledge of biodiversity change at the local scale is in some senses better and in some senses worse than our knowledge at global and regional scales. Local-scale vegetation plots are by definition small (most often $\leq 1,000$ m²; 111), such that there is far less uncertainty involved in estimating species presence or abundance. There have been hundreds of studies following local-scale temporal vegetation change in a wide range of habitat types and geographic regions. However, local studies are typically of short duration (rarely > 50 years), and essentially none cover the entire Anthropocene. In this section, we first summarize a recent meta-analysis focusing on observed trends in repeated vegetation surveys. Subsequent subsections review (nonexhaustively) the major hypothesized drivers of biodiversity change, in each case drawing on both space-for-time and experimental studies.

Temporal Plant Biodiversity Trends in Resurvey Studies

Vellend et al. (111) systematically searched the literature for studies reporting estimates of plant diversity in one or more local-scale plots [≤ 5 hectares (ha) for trees, ≤ 1 ha otherwise] surveyed at least twice over a period of at least five years. The data set (later updated to the end of 2014; 113) includes studies from all continents except Antarctica, but with an underrepresentation of tropical regions. The main result across 212 studies is that the distribution of temporal trends is centered on zero, regardless of habitat type or geographic region (**Figure 2**). Some individual studies reported substantial increases in plant richness over time (e.g., +38% in forests and grasslands of Vancouver Island between 1968 and 2009; 64), whereas other studies reported substantial decreases in richness over time (e.g., -70% in the Siskiyou Mountains of Oregon between 1950 and 2007; 17). Most studies reported very little temporal change in either direction ($< 10\%$).

The observational data reported by Vellend et al. (111) provide limited scope for assessing underlying causes and cover almost exclusively the twentieth and twenty-first centuries. All of the individual studies concerned sites that had not undergone major land-use transitions during the period of study. However, many studies were conducted in anthropogenically altered habitats (e.g., pastures or urban areas) or had been subject to disturbances of various kinds—climate change, species invasions, etc. In other words, although this was not a sample of pristine sites, the sites remained the same habitat type during the period of study, consistent with the original motivation to combine the results with experimental studies of how biodiversity influences ecosystem functions, essentially all of which share this feature (39). As described below, major land-use transitions often cause major losses to local-scale plant diversity (69). What the results of Vellend et al. (111) suggest is that in the absence of major land-use transitions, local-scale plant diversity in any given ecosystem has been just as likely to increase as it has been to decrease over the past century or so,

Ecosystem functions: properties of ecosystems related to the stocks and flows of energy and matter, such as productivity and nutrient cycling

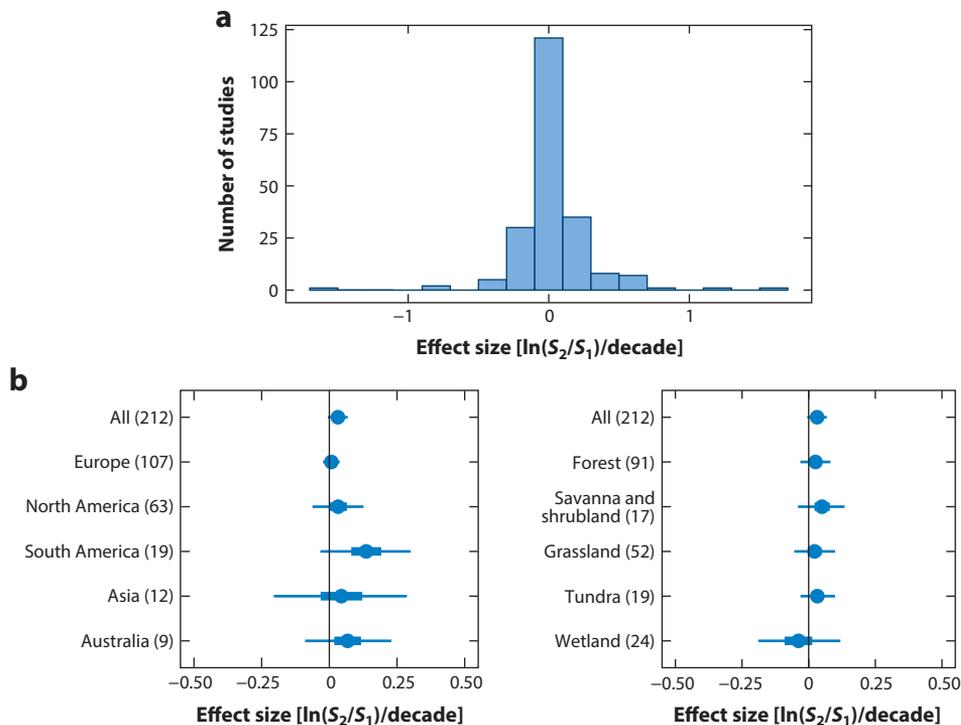


Figure 2

Local-scale temporal change in plant species richness in 212 studies of 5–261 years' duration. Temporal change is expressed as the log ratio of species richness for the last year of surveys (S_2) and the first year (S_1) per decade. (a) Histogram of all studies. (b) Mean \pm 95% credible intervals for different geographic regions and habitat types, with the number of studies shown in parentheses. Not shown in this panel are two studies from Africa with a raw mean effect size of 0.165. Data were compiled from the published literature as reported in References 111 and 113.

with many places showing no significant temporal trend at all. Exceedingly few local-scale data are available to assess changes prior to the twentieth century, with relatively few for even the first part of the twentieth century.

Effects of Land Use

Large areas of the earth's surface have been converted from primary vegetation to anthropogenic habitats. Newbold et al. (69) compiled data from >250 space-for-time studies to assess the local-scale consequences of land use for biodiversity in a range of animal and plant taxa. Here, we focus on results that apply to plants (T. Newbold, personal communication), of which the clearest was that local species richness was ~30% lower on agricultural lands (by far the dominant human land use) than it was in minimally disturbed primary vegetation.

Urban areas occupy a very small portion of the earth's surface, but roughly half of the human population lives in them. Suburban yards or urban areas devoid of green spaces typically have a lower species richness than primary vegetation, but larger, managed urban green spaces have an average species richness similar to that in primary vegetation (69). Consistent with these results, a

Habitat

fragmentation: the process by which a large area of natural habitat is divided into smaller fragments

negative correlation between the magnitude of human presence in cities (e.g., population density) and plant species richness has been observed for small study plots, but in units of observation larger than 1 km², species richness actually increases as a function of human impact (75). The latter result could be due to the tendency of humans to settle in areas already high in biodiversity or to positive effects of human-caused environmental heterogeneity and species introductions. The latter conclusion is supported by increases in city-wide plant species richness in recent centuries caused specifically by introduced neophytes (48).

In primary vegetation and successional sites no longer under intense land use, anthropogenic activities such as logging and bushmeat hunting did not have a significant impact on local species richness (69). Similarly, a meta-analysis aimed specifically at assessing the effect of logging of various intensities on local plant biodiversity in temperate forests found no significant effect on average (25). For plants, species richness was not significantly lower in secondary vegetation (of any age) than in primary vegetation, although the qualitative trend was of reduced diversity (T. Newbold, personal communication).

In sum, when people destroy primary vegetation to make way for agriculture and urbanization, local-scale plant biodiversity declines. Less intensive land uses, such as logging, might have positive or negative effects in any given case. When land is no longer used for agriculture, local biodiversity tends to increase, often to levels similar to those observed in primary vegetation.

Effects of Habitat Fragmentation

Studies of habitat fragmentation focus not on the areas converted to a new land use but on the smaller habitat patches left behind. Distinguishing an effect of fragmentation per se from an effect of habitat loss requires comparing habitat fragments to equal-area portions of larger habitats (28). Two kinds of alteration to habitat patches that can be unambiguously attributed to fragmentation per se are increased spatial isolation from other similar habitats and the creation of edges between a focal habitat (e.g., forest) and an anthropogenic habitat (e.g., crop field).

The most famous study of habitat fragmentation involved the experimental creation of forest fragments of 1 ha, 10 ha, and 100 ha in the Amazon rain forest and the measurement of many ecological variables over the subsequent >30 years (53). When the investigators ensured equal sample effort or plot area, small fragment size led to sharp declines in the diversity of several taxa—most dramatically birds (100)—but not generally for plants. The smallest fragments showed greatly increased tree mortality and rapid community turnover, but the species richness of trees in 1-ha plots was not influenced by fragment size (54). There was also no significant decline in the diversity of palms (90) or ant-dispersed understory plants (11), but there was a significant decline for epiphyllous bryophytes (129). Other studies of tropical forest fragments have focused on functional or phylogenetic plant diversity, finding increases, decreases, or no change with fragment size, depending on the metric used or the specific context (1, 61, 85). Given that the generation time of most trees exceeds the duration of these studies, the longer-term consequences of tropical forest fragmentation remain uncertain.

There is considerable variation among studies testing the effects of fragmentation on plants (41). Fragment isolation is most often found to have a negative effect on species richness (**Figure 3a**), whereas edges have strong positive effects more often than strong negative effects (**Figure 3b**). Ibáñez et al. (41) began their meta-analysis by classifying effects as positive or negative regardless of the effect size, but looking at the underlying data shows that many effects are quite close to zero (**Figure 3**). This result is consistent with other cross-taxon reviews of habitat fragmentation (22, 28).

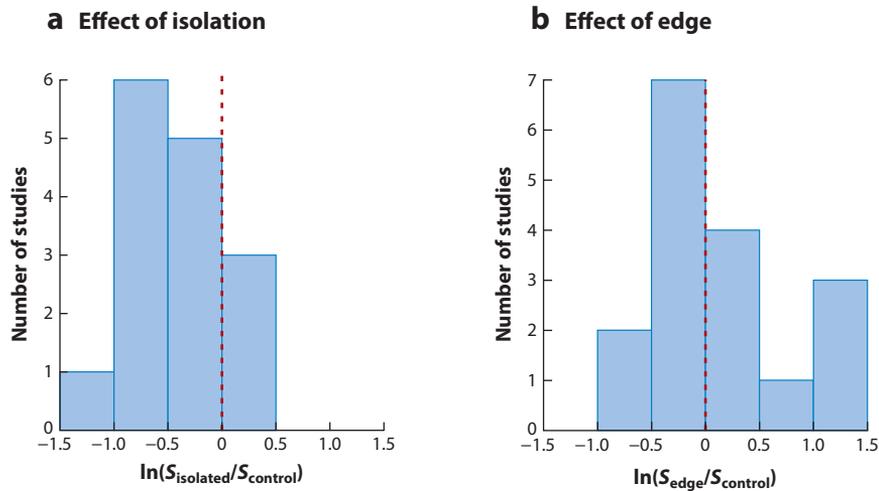


Figure 3

Distributions of effect sizes of (a) patch isolation and (b) proximity to patch edges on plant species richness (S). Data are from Reference 41.

Effects of Climate Warming

Climate is the primary determinant of global vegetation patterns (119), and changing climatic conditions can cause extinctions of some species (107) at the same time that it creates suitable conditions for others (74). Across many studies, spatial variation in regional- and local-scale plant species richness is best predicted by variables calculated from climate data, such as potential evapotranspiration (30). The effect of temperature on regional-scale plant species richness varies from strongly positive in mesic or humid portions of the earth to strongly negative in severely water-limited areas (94). Therefore, the regional capacity for plant species richness will likely increase with climate warming in temperate and polar regions while decreasing in dry tropical regions by the year 2100 (94).

Relationships between climate and species richness at local scales tend to be similar to those at larger scales (34, 49, 86) (see **Figure 4**), if somewhat weaker in magnitude (30). Using space-for-time substitution, we can thus make a prediction that climate warming should increase local plant diversity in cool and mesic or humid regions and decrease diversity in drier regions. This is consistent with some explicitly temporal observational studies, which have found that local richness increases in temperate mountainous areas and that diversity declines with reduced rainfall or increased temperature in water-limited grasslands (14, 37, 71, 74, 86, 104) (see **Figure 4b**).

Many field experiments have manipulated temperature and/or precipitation, although multi-habitat meta-analyses have not included species diversity as a response variable (4, 58, 128). Our qualitative review of experimental warming studies suggests that effects on plant species diversity are context dependent and highly variable from study to study. We focus largely on temperature manipulations, given the near ubiquity of predicted temperature increases across the globe.

Experimental warming, typically of $\sim 1\text{--}2^\circ\text{C}$, seems most often to have no effect on species richness or diversity (e.g., 27, 77, 130), although some studies have reported warming-induced declines (e.g., 46). In six shrubland sites in Europe, Peñuelas et al. (77) experimentally imposed both warming and drought, finding no significant effects on plant species richness after seven years except at one site in Spain, where there was a negative effect of drought. Elmendorf et al.

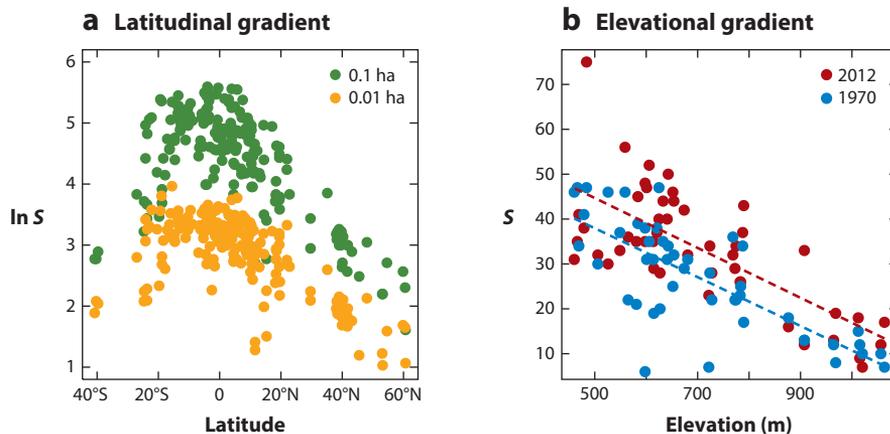


Figure 4

Patterns of local-scale forest plant diversity along putative climatic gradients, showing increased species richness (S) at relatively warm places and times. (a) Trend with latitude for trees. The data show averages in individual 0.01-hectare (ha) plots (orange) or the sum across ten such nearby plots (green). (b) Trend with elevation for all vascular plants, including linear regressions (dashed lines). The data come from 20×20 m or 20×40 m plots on Mont Mégantic in southern Québec, Canada, both before (blue) and after (red) a period of $\sim 1.5^\circ\text{C}$ climatic warming. Data in panel *a* are from Reference 34, as reported in Reference 49; data in panel *b* are from Reference 86.

(27) reported no overall effect of experimental warming on species diversity (Simpson index) over up to 20 years at 61 tundra sites. By contrast, reduced species richness or diversity caused by experimental warming was found in Tibetan grassland and shrubland (46) and in a New England salt marsh (33).

Both space-for-time and experimental studies predict effects of warming that are highly variable from site to site. However, the space-for-time prediction of increased local diversity caused by warming in mesic or humid sites has not generally been borne out in experiments, despite some support for this prediction from observational studies (71, 74, 86). One possible explanation is that instantaneous environmental change imposed by experiments might not mimic the effects of more gradual warming in nature (47, 93) and might cause declines in some species more rapidly than can be offset by colonization of new species during a short-term study. More generally, the space-for-time prediction represents a long-term expectation, and for perennial plant communities (i.e., most plant communities) the lag time of response may well be on the order of many decades or even centuries (43). Given the very general and strong spatial relationships between climate and plant diversity, it seems reasonable to expect climate warming to cause local plant diversity to decline, on average, in water-limited regions, at the same time that it increases elsewhere.

Effects of Nitrogen Input

Nitrogen (N) is a key limiting nutrient for plant growth, and anthropogenic N additions to the biosphere via the burning of fossil fuels and fertilizer production have increased dramatically during the Anthropocene (32). The effects of N addition are especially amenable to manipulative experiments. Many experiments apply a high N input over a short period of time, with uncertain implications for understanding the consequences of long-term inputs of lower magnitude (7),

although there is clear evidence that N is a cause of declining local plant biodiversity, as described below.

Many N-addition experiments have led to declines in local-scale plant richness and diversity, with the most striking and consistent results in temperate grasslands (7, 15, 20). Outside of temperate grasslands, N addition almost always causes shifts in species composition (e.g., favoring nitrophilous species) and most often causes increased biomass production, but effects on species diversity and richness are highly variable, with increases in diversity possible, if quite rare (9). The main mechanisms underlying diversity loss appear to be (a) dominance achieved by one or a few species that are strongly favored by increased N availability, leading to the competitive exclusion of others, and (b) soil acidification (7).

Space-for-time studies of N deposition have been conducted less often than experimental N additions. In European grasslands, Stevens et al. (97) found a sharp decline in local-scale plant species richness with increasing N deposition. Across a broad range of vegetation types in the United States, Simkin et al. (91) found strong context dependence of N-deposition effects and confirmed the generally negative effect of N deposition in grasslands and other open habitats, especially on acidic soils. However, when they looked within particular vegetation types (most relevant to making space-for-time inferences), they found that 36.5% showed a negative effect of N deposition on plant richness, 45.5% showed no effect, and 18% showed a positive effect. Local plant species richness is expected to increase with N deposition in relatively cool habitats, on soils with high pH, and where current N deposition is relatively low (91).

Overall, the evidence indicates that N deposition has caused and will likely continue to cause loss of local plant diversity in temperate grasslands and possibly other habitats. However, the effects of N deposition are highly variable across the planet, and it often has no effect on local plant diversity, or even positive effects in some cases.

Local-Scale Conclusions

- Conversion of primary vegetation to intense agricultural or urban use tends to cause a decline in local plant biodiversity.
- The effects of other major drivers of plant community change—resource extraction, habitat fragmentation, climate warming, and N deposition—are all highly context dependent.
- Outside of wholesale agricultural or urban habitat conversion, high context dependence and potentially counteracting forces create massive variation from place to place in temporal plant biodiversity trends, with many places showing increases, decreases, or little or no change.
- Substantial uncertainty about long-term changes of diversity at local scales remains because of a lack of local-scale studies that span the Anthropocene.

PLANT BIODIVERSITY CHANGE ACROSS SCALES

The results discussed above indicate that plant biodiversity changes during the Anthropocene show clear scale dependence (**Figure 5**). At the global scale, the Anthropocene has seen relatively few documented plant extinctions to date and a nontrivial number of speciation events, with the future long-term net trend likely to be negative. At the regional scale, nonnative species establishment has far outweighed extinction in the regions that have been studied, although weaker or even negative regional trends are possible for poorly studied tropical continental areas. Both the magnitude and direction of local-scale plant biodiversity change have varied tremendously from place to place (**Figure 5**).

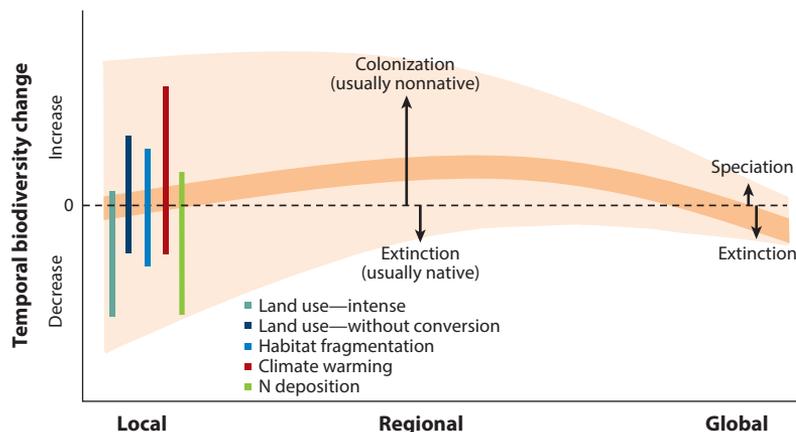


Figure 5

Schematic illustrating the key empirical results concerning plant biodiversity change during the Anthropocene at different spatial scales. The large shaded polygon represents the range of possible outcomes, with the central tendency indicated by the thick, darker curve. Colored bars represent the range of local-scale outcomes of different drivers of change; context dependence creates wide variation for each driver, and combinations of drivers might push diversity change further than any one driver, in either direction. The height of each arrow represents the relative direction and strength of the process indicated.

The combination of extinctions of species native to particular continents or islands and the widespread colonization of many nonnative species suggests that distant regions (e.g., different continents) must be becoming more similar in species composition. This phenomenon has been dubbed biotic homogenization, and indeed many studies have shown evidence of it (5). When comparing continents such as North America and Europe, for example, Winter et al. (123) found that nonnative plant species caused homogenization. Within continents or at smaller spatial scales, changes in compositional similarity have been highly variable from study to study. For example, nonnative species have caused regions (typically countries) within Europe to actually diverge in species composition, whereas regions of North America have shown homogenization (123). Temperate urban areas share many cosmopolitan plant species and thus have shown clear biotic homogenization (50), and in any particular landscape in Europe, forests have sometimes shown homogenization, sometimes differentiation, and sometimes no change in compositional similarity in recent decades (3). Species composition varies tremendously among different land uses (69), such that within a typical mixed landscape of primary vegetation, secondary vegetation, and various forms of agriculture, spatial variation in species composition is almost certainly higher than it would have been in a pre-Anthropocene landscape dominated by primary vegetation. In short, the Anthropocene has seen both biotic homogenization and differentiation, depending on scale and context, with the only likely generalization being that intense human land use and nonnative species introductions have caused species composition to converge across continents and to diverge among different land uses within landscapes.

Biotic homogenization:

increasing similarity in species composition among regions or sites, most often ascribed to nonnative species introductions

IMPLICATIONS FOR CONSERVATION

The concept of biodiversity is tightly linked both historically and thematically with conservation biology (63, 101, 121), and the results of this review speak to several important conservation questions.

First, counter to the biodiversity-crisis narrative, many regions of the earth have actually seen a net gain in plant richness during the Anthropocene, largely because of the establishment of nonnative species. Such increases in biodiversity are still considered a problem if a conservation goal is to prevent declines of native species specifically. On the surface, it is paradoxical that an increase in biodiversity would not be welcomed by a discipline whose aim is the protection and maintenance of biodiversity. The resolution of this paradox comes from the fact that the perceived problem is actually not one of biodiversity per se, but of the species composition of the flora. Focusing on native species is a normative judgment, not one based on science, and it is crucial to make this distinction clear when articulating the rationale behind conservation philosophies and actions (18). Both observational and experimental studies almost universally find shifts in species composition in response to various drivers of change, but the response of biodiversity per se is far less predictable or consistent.

The issue of species composition versus species diversity as targets of conservation comes into clear focus in the case of anthropogenic disturbances, such as logging and habitat fragmentation, both of which are widely considered to be threats to biodiversity. Conservation efforts often focus on preserving or restoring the conditions found in undisturbed habitats, such as old-growth forests, but not typically because such forests harbor greater local plant biodiversity. The only general observation one can make is that disturbances such as logging favor early successional species (e.g., those that require perturbed soil to germinate or high light to grow) over late successional species (e.g., shade-tolerant, slow-growing trees), thus prompting a shift in species composition. However, a large number of early successional species can sometimes increase local plant diversity relative to undisturbed sites in just a few years after logging (36, 76), while in other cases local plant diversity remains lower in successional forests for many decades (35). More generally, both natural and anthropogenic disturbances can have positive, negative, hump-shaped, or nonsignificant effects on the biodiversity of many different taxa (60). In short, factors such as logging or fragmentation might decrease the conservation value ascribed to a given site by people, but this is not necessarily accompanied by a decline in plant biodiversity.

In recent years, an additional major focus of ecologists and conservation biologists has been ecosystem services—benefits that humans derive from nature—as a target of conservation efforts, and the possibility that ecosystem services depend on biodiversity. The argument that ecosystem functions or services depend on biodiversity has a scientific basis, largely in the form of experimental studies manipulating plant species richness in small study plots (39). However, there are some important nuances and context dependencies that restrict the application of this argument to justify biodiversity conservation. First, because biodiversity is generally increasing for plants at regional scales, concerns about declines (at least of total biodiversity) at these scales are not applicable. Second, the primary scenario in which we see consistent and predictable declines in local diversity—and therefore where this argument should be most applicable—is the conversion of land to agricultural use. But the reduction of plant diversity in crop fields is not an incidental consequence of land use. Rather, people aim to maximize one ecosystem service—food production—by deliberately creating simplified ecosystems with one or a few crop species (26). Intensive agriculture can certainly come at a cost to other ecosystem services, such as carbon storage and water quality (66), but even here it is doubtful that the underlying cause is decreased biodiversity, rather than yearly harvesting and plowing, or habitat conversion (i.e., replacing a forest with an annual-dominated system).

Outside of agricultural fields, major declines in plant biodiversity are not especially common (**Figure 2**), so arguments about compromised ecosystem function based on biodiversity loss pertain only to some sites. That being said, the importance of native species diversity specifically for ecosystem function is still not well understood. There is experimental evidence to suggest that

Normative:

an adjective used to describe widely agreed upon values or standards

interacting plant species can evolve rapidly in ways that promote ecosystem function (e.g., 131), but it is unclear how important hundreds, thousands, or millions of years might be in shaping how native assemblages function. One fairly restricted domain in which specific management actions are clearly justified by a link between biodiversity and ecosystem function involves habitats such as tree plantations or restoration projects, where people directly control local biodiversity (106, 116). An important and rarely asked question concerns the impact of increasing local biodiversity for the many systems where this has occurred.

Overall, the tendency toward increases in regional-scale plant biodiversity and highly variable local-scale trends during the Anthropocene challenge conservation biologists to specify more clearly the precise goals of conservation actions (e.g., diversity versus composition), whether these goals stem from normative judgments or scientific evidence, and the degree to which scientific evidence relates directly to particular conservation actions.

FROM CURRENT KNOWLEDGE TO FUTURE RESEARCH

At all scales, our knowledge of plant biodiversity changes during the Anthropocene is especially poor in tropical continental regions. Compiling and exploiting any and all available historical data on plant communities in the tropics is an important research priority. Our ability to study the past is limited by the availability of historical data, but forward-looking biodiversity monitoring studies are straightforward to implement, if extremely challenging to generate funding for. Long-term monitoring of plant communities in all habitat types is needed in order to understand the causes and consequences of Anthropocene plant biodiversity change. Biodiversity change in response to a given driver is subject to time lags, both for extinction and for colonization (43), and only by following communities over the long term can we assess the time course of such changes.

This review focuses on roughly the past 500 years, but ecological impacts of human land use extend back in time thousands of years, with important consequences for interpreting more recent human impacts. Pre-Anthropocene human impacts were likely localized compared with those of the present day, although they may have covered a broader swath of terrestrial ecosystems than is generally appreciated (8). For example, human land use changes initiated upward of 1,000 years ago may well be the cause of relatively high contemporary plant biodiversity in systems such as European heathlands and grasslands (73), where modern land-use intensification has caused declines (73, 99). Better integration of studies from the Holocene and the Anthropocene can help contextualize and provide important nuance to site-specific conservation implications of recent biodiversity trends.

Predicting future biodiversity change presents massive challenges, especially for regions undergoing rapid economic development. At regional scales, conversion of primary vegetation to anthropogenic uses is clearly one of the main drivers of extinctions (78). However, as we have seen for the temperate zone, expansion of agriculture and resource extraction also increase environmental heterogeneity and are typically associated with nonnative species introductions, both of which can contribute to increasing regional diversity. Predicting the net result of these forces in both temperate and tropical regions will require the integration of many lines of evidence: studies of the potential pool of nonnative colonists to a given region, estimates of their probability of arrival and establishment, the development of robust projections of future land use, improved understanding of likely changes in climate, and more reliable estimates of future extinctions, including models that can account for the small number of extinctions observed to date. Filling these needs presents a daunting task, but developing such models and confronting them with data in the future will provide an improved basis for predicting the future of plant life on earth.

SUMMARY POINTS

1. At the global scale, the rate of plant extinctions has increased during the Anthropocene relative to background levels, but the total number of these extinctions has been far fewer than predicted by some models, while plant speciation may have accelerated.
2. The available data support, but do not conclusively demonstrate, the assertion that the number of plant species globally has declined during the Anthropocene, but future declines seem likely given current and pending threats.
3. At the regional scale, the number of nonnative plant species established exceeds the number of native species that have gone extinct, often by a large margin, especially on islands.
4. At the local scale, conversion of primary vegetation to crop fields or urban development typically causes plant biodiversity to decline.
5. Outside of situations of wholesale habitat conversion for human use, recent temporal trends in local plant biodiversity are highly variable, sometimes positive, sometimes negative, and often of negligible magnitude.
6. Major drivers of global environmental change, such as habitat fragmentation, climate change, and nitrogen deposition, have effects on local plant biodiversity that are highly context dependent, both in magnitude and in direction.
7. The kinds of local or regional biotic changes that often concern conservation biologists—e.g., declines in native species and increases in nonnative species—do not necessarily involve declines in biodiversity per se, but rather represent changes in species composition.

DISCLOSURE STATEMENT

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Contents

Firmly Planted, Always Moving <i>Natasha V. Raikhel</i>	1
Biogenesis and Metabolic Maintenance of Rubisco <i>Andreas Bracher, Spencer M. Whitney, F. Ulrich Hartl, and Manajit Hayer-Hartl</i>	29
The Epigenome and Transcriptional Dynamics of Fruit Ripening <i>James Giovannoni, Cuong Nguyen, Betsy Ampofo, Silin Zhong, and Zhanjun Fei</i>	61
Retrograde Signals: Integrators of Interorganellar Communication and Orchestrators of Plant Development <i>Amancio de Souza, Jin-Zheng Wang, and Katayoon Debesb</i>	85
The Structural Basis of Ligand Perception and Signal Activation by Receptor Kinases <i>Ulrich Hohmann, Kelvin Lau, and Michael Hotborn</i>	109
Cell Biology of the Plant Nucleus <i>Iris Meier, Eric J. Richards, and David E. Evans</i>	139
Phloem-Mobile RNAs as Systemic Signaling Agents <i>Byung-Kook Ham and William J. Lucas</i>	173
Chemical Genetic Dissection of Membrane Trafficking <i>Lorena Norambuena and Ricardo Tejos</i>	197
Plant Mitochondrial Genomes: Dynamics and Mechanisms of Mutation <i>José M. Gualberto and Kathleen J. Newton</i>	225
Plastoglobuli: Plastid Microcompartments with Integrated Functions in Metabolism, Plastid Developmental Transitions, and Environmental Adaptation <i>Klaas J. van Wijk and Felix Kessler</i>	253
Strigolactone Signaling and Evolution <i>Mark T. Waters, Caroline Gutjahr, Tom Bennett, and David C. Nelson</i>	291
Zooming In on Plant Hormone Analysis: Tissue- and Cell-Specific Approaches <i>Ondřej Novák, Richard Napier, and Karin Ljung</i>	323

Guilt by Association: A Phenotype-Based View of the Plant Phosphoinositide Network <i>Katharina Gerth, Feng Lin, Wilhelm Menzel, Praveen Krishnamoorthy, Irene Stenzel, Mareike Heilmann, and Ingo Heilmann</i>	349
The Life and Death of a Plant Cell <i>Mehdi Kabbage, Ryan Kessens, Lyric C. Bartholomay, and Brett Williams</i>	375
Genomics, Physiology, and Molecular Breeding Approaches for Improving Salt Tolerance <i>Abdelbagi M. Ismail and Tomoaki Horie</i>	405
New Strategies and Tools in Quantitative Genetics: How to Go from the Phenotype to the Genotype <i>Christos Bazakos, Mathieu Hanemian, Charlotte Trontin, José M. Jiménez-Gómez, and Olivier Loudet</i>	435
Novel Insights into Tree Biology and Genome Evolution as Revealed Through Genomics <i>David B. Neale, Pedro J. Martínez-García, Amanda R. De La Torre, Sara Montanari, and Xiao-Xin Wei</i>	457
Defense Priming: An Adaptive Part of Induced Resistance <i>Brigitte Mauch-Mani, Ivan Baccelli, Estrella Luna, and Victor Flors</i>	485
Trade-Offs Between Plant Growth and Defense Against Insect Herbivory: An Emerging Mechanistic Synthesis <i>Tobias Züst and Anurag A. Agrawal</i>	513
The Role of Plant Innate Immunity in the Legume-Rhizobium Symbiosis <i>Yangrong Cao, Morgan K. Halane, Walter Gassmann, and Gary Stacey</i>	535
Plant Biodiversity Change Across Scales During the Anthropocene <i>Mark Vellend, Lander Baeten, Antoine Becker-Scarpitta, Véronique Boucher-Lalonde, Jenny L. McCune, Julie Messier, Isla H. Myers-Smith, and Dov F. Sax</i>	563

Errata

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