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Daniel E. Bunker, *et al.*
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Species Loss and Aboveground Carbon Storage in a Tropical Forest

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Tropical forest biodiversity is declining, but the resulting effects on key ecosystem services, such as carbon storage and sequestration, remain unknown. We assessed the influence of the loss of tropical tree species on carbon storage by simulating 18 possible extinction scenarios within a well-studied 50-hectare tropical forest plot in Panama, which contains 227 tree species. Among extinction scenarios, aboveground carbon stocks varied by more than 600%, and biological insurance varied by more than 400%. These results indicate that future carbon storage in tropical forests will be influenced strongly by future species composition.

In terrestrial ecosystems, functional diversity and relative abundance influence both the magnitude (1–5) and variability (6) of aboveground biomass. Aboveground biomass, in turn, substantially determines an ecosystem's potential for carbon storage, which plays an important role in the regulation of atmospheric CO₂ and global climate change (7, 8). Biodiversity, however, is changing rapidly in response to a variety of anthropogenic drivers (9–13). The potential for terrestrial carbon sequestration could be altered sharply by ensuing changes in species composition.

The relationship between diversity and aboveground biomass has been examined in herbaceous ecosystems such as grasslands (3–6), meadows (14), and wetlands (15). These ecosystems, however, account for just 16% of the estimated 558 Pg (1 Pg = 10¹⁵ g) of carbon stored in vegetation (16). The remaining 470 Pg of carbon reside in forests, woodlands, and savannahs, more than half (54%) of which are tropical.

In tropical forests, conventional biodiversity manipulations are prohibitively costly because of the large number of tree species as well as the size and longevity of tropical trees. Instead, we simulated species extinctions in a diverse tropical forest by using data from the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panama (17). Our model, which expanded on the approach of Solan and col-

leagues (18), enabled us to establish many species combinations and compositions under different extinction scenarios to explore the realm of possible futures for aboveground carbon storage. We simulated these effects on aboveground biomass by removing species with a probability proportional to extinction-related traits (e.g., small population size) and replacing the eliminated basal area with a random draw from the remaining community (Fig. 1) (19). We used functional traits [wood density and volume per unit basal area; see equation S1 in (19)] to quantify the aboveground carbon pool for each simulated community. Thus, variation in functional diversity (the diversity of these functional traits among species) governs ecosystem response.

We explored three classes of trait-based extinction scenarios that represent a broad spectrum of extinction mechanisms (table S1). One class consists of extinction associated with population traits such as low population growth rates, low densities, and endemism, which are known correlates of extinction risk (20–22). The second class consists of extinction scenarios related to management or harvest strategies, such as selective harvest for hardwoods or harvesting the most common or the largest trees; this scenario uses related traits such as wood density, stature, and abundance. The third class consists of species' responses to environmental change, such as changes in precipitation, rates of disturbance, or elevated CO₂ (23, 24). We also included a random extinction scenario that serves as a reference and reflects the approach commonly used in combinatorial biodiversity experiments.

The extinction scenarios produced divergent effects in both the magnitude and variability of aboveground carbon storage (Fig. 2 and table S1). For instance, the extinction of species with the lowest wood density led to strong increases (+75%) in carbon storage (Fig. 2, G to I, and table S1), whereas the loss of species that attain large stature resulted in a

strong decline in carbon stocks (Fig. 2, D to F, and table S1). Extinction scenarios demonstrated different degrees of loss of biological insurance (i.e., decreasing predictability or increasing variability as species are lost) (Fig. 2). For instance, the loss of endemic species resulted in relatively less loss of biological insurance, largely because endemics tend to be locally rare and contribute little to total carbon stocks (Fig. 2, S to U, and table S1). These differences in loss of biological insurance are attributable to the extent of variability in functional traits, which is strongly dependent on species identity and community composition.

Anthropogenic effects on tropical forest diversity vary widely. Selective logging typically removes a small number of species from a community (25), whereas conversion to forest plantations removes all but one or two species. Our results show that selective logging for

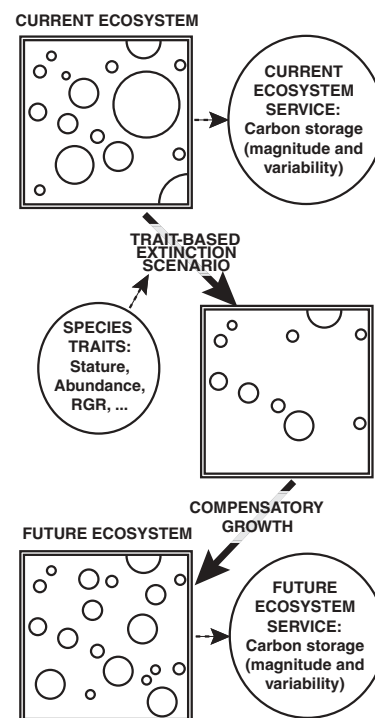


Fig. 1. Impact of tree-species extinctions on carbon storage within an extant tropical forest. Ellipses represent input and output variables, solid arrows represent process steps, and squares represent the three states of the BCI 50-ha forest plot, in which circles represent trees of different diameter and species identity. On the basis of the relationship between known composition and relative abundance of trees in the 50-ha plot and current aboveground carbon storage (top), future carbon storage (bottom) can be estimated under different extinction scenarios. Extinction scenarios use trait-based responses to environmental change (e.g., habitat fragmentation and elevated CO₂). The middle square represents the transitory state in which extinction has led to reduced abundance. After compensatory growth that replaces basal area lost to extinction, plant traits are used to estimate the ecosystem service of a less diverse forest. RGR, relative growth rate.

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species with high wood density, large diameter, high basal area, or maximal wood volume will likely lead to overall declines in carbon storage of 70, 29, 17, and 21%,

respectively (Fig. 2 and table S1). In contrast, conversion to plantations that use species with high wood density may increase aboveground carbon storage by up to 75% if

never harvested (Fig. 2, G to I, and table S1). However, conversion to plantation may cause decreases in belowground carbon and reduce other ecosystem services such as fruit production or water quality.

In addition to direct anthropogenic forces, changes in forest composition have been observed in natural forests of the Amazon, where increased stem turnover and liana abundance may favor fast-growing species (24, 26, 27). Our results suggest that if this trend persists, a shift toward fast-growing species in tropical forests could lead to a 34% decrease in carbon storage (Fig. 2, M to O, and table S1). Climate observations and model predictions (28, 29) both suggest continued decreases in precipitation over much of the humid tropics. Our model predicts a slight increase in carbon stocks (10%), with a shift toward drought-tolerant species, and notably, a 48% increase in the loss of biological insurance relative to random extinction (Fig. 2, P to R, and table S1). Thus, species diversity may provide increased biological insurance in the face of species loss due to reduced precipitation.

Our results should not be interpreted as specific predictions for future carbon storage but rather as an assessment of the relative effects of nonrandom species losses. Drivers of biodiversity change will likely alter additional mechanisms that regulate carbon storage. For example, disturbances caused by selective logging decrease carbon storage in the short term, whereas increased precipitation may increase carbon storage through effects on net primary productivity. In addition, because we based our species-poor communities on the observed composition and basal area of the BCI plot, the retained species maintain their relative abundance and size-frequency distributions within these impoverished communities. For this reason, to the extent that complementarity, facilitation, and sampling effects (30–32) occur in the intact 50-ha plot, these forces have equivalent effects in our simulated communities and are invariant

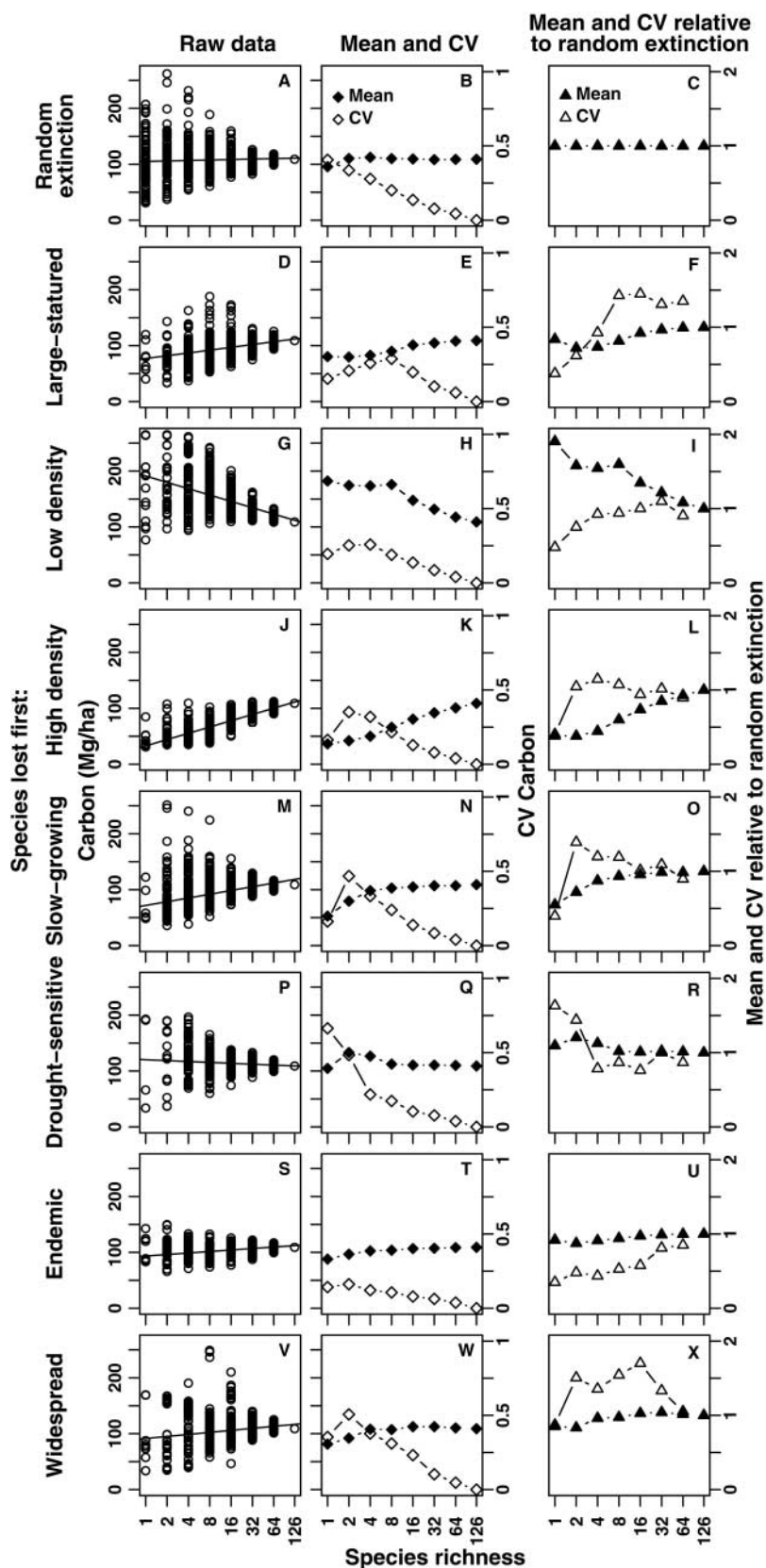


Fig. 2. Representative results of simulated influences of biodiversity on aboveground carbon storage in the 50-ha Forest Dynamics Plot on BCI, Panama. The intact community included 126 species; the x axes have a \log_2 scale. The left panels show simulation results (open circles) and linear fit (solid line) of the effect of \log_2 species richness on aboveground carbon storage. The center panels show the mean (solid diamonds) and coefficient of variation (CV) (open diamonds) of carbon storage. The right panels show the mean (solid triangles) and CV (open triangles) of carbon storage relative to random extinction. (A to C) Random extinction. (D to F) Large-statured species lost first. (G to I) Species with low wood density lost first. (J to L) Species with high wood density lost first. (M to O) Slow-growing species lost first. (P to R) Drought-sensitive species lost first. (S to U) Endemics lost first. (V to X) Widespread species lost first. Values are lower than those reported elsewhere because we excluded 101 species (21% of aboveground carbon) for which we lacked wood-density data.

with species richness. If complementarity, facilitation, and sampling effects do contribute to positive effects of diversity on carbon storage on BCI, as often has been observed in simpler communities (1–5), then actual carbon storage in species-poor communities may be lower than our models predict. Indeed, high diversity within the BCI plot may reduce losses of carbon to density-dependent effects of herbivores and pathogens (33, 34).

Species extinctions are rarely random but rather are driven by the interaction between species traits and environmental change. Our results show that tropical forest carbon storage depends on species composition and on the mode and manner in which species are lost. By extension, carbon storage in reforested landscapes depends especially on the functional diversity of the available species pool. Because variability decreases with species richness, and because extinction scenarios differ widely in magnitude and direction, management options that favor high diversity will maximize predictability for tropical forest carbon storage and sequestration.

We have examined only one of many ecosystem services provided by tropical forests. Extinction scenarios that maximize carbon storage may minimize other services such as flood protection, nutrient retention, cultural services, pollination, biological control, and provisioning of fruits, nuts, and bush meat (10). Human

domination of terrestrial and aquatic landscapes has made us increasingly dependent on a reduced number of species to provide critical ecosystem services. Given uncertainty in both the nature of extinction and the variety of ecosystem services required for human well-being, we may best be able to meet these demands by maximizing the pool of species on which we depend.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/1117682/DC1
Materials and Methods

Table S1

References

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The Pseudo-Response Regulator *Ppd-H1* Provides Adaptation to Photoperiod in Barley

Adrian Turner,* James Beales,* Sébastien Faure, Roy P. Dunford, David A. Laurie†

Plants commonly use photoperiod (day length) to control the timing of flowering during the year, and variation in photoperiod response has been selected in many crops to provide adaptation to different environments and farming practices. Positional cloning identified *Ppd-H1*, the major determinant of barley photoperiod response, as a pseudo-response regulator, a class of genes involved in circadian clock function. Reduced photoperiod responsiveness of the *ppd-H1* mutant, which is highly advantageous in spring-sown varieties, is explained by altered circadian expression of the photoperiod pathway gene *CONSTANS* and reduced expression of its downstream target, *FT*, a key regulator of flowering.

Plants have evolved sophisticated controls to ensure that flowering occurs when there is the greatest chance of pollination, seed de-

velopment, and seed dispersal. Usually this involves restricting flowering to a specific time of year. To achieve this, many plants use photoperiod as an environmental cue to regulate development. The timing of flowering has important impacts on crop yield, and the modification of responses to environmental cues by human selection has been central to the success and spread of agriculture.

The control of flowering by photoperiod is understood best in the long-day (LD) dicot *Arabidopsis* and the short-day (SD) monocot cereal rice. In *Arabidopsis*, expression of *GIGANTEA* (*GI*) and *CONSTANS* (*CO*) is regulated by the circadian clock such that coincidence of the *CO* expression peak with light only occurs in LD conditions. Light-stabilized *CO* protein is a transcription factor inducing downstream genes, including *FLOWERING LOCUS T* (*FT*) (1, 2).

In rice, analyses of natural variation showed that *Heading date1* (*Hd1*), a major determinant of photoperiod response, is an ortholog of *CO* (3), that *Hd3a* is an ortholog of *FT* (4), and that *GI* is also conserved (5). However, the interaction of *Hd1* with *FT* is altered such that *FT* expression is inhibited in LDs (2, 5). The rice *Ehd1* gene also controls photoperiod response but has no direct counterpart in *Arabidopsis* and regulates *FT* independently of *Hd1* (6). Photoperiod response in rice therefore has conserved and novel aspects compared with *Arabidopsis*, but in both species increased *FT* expression is crucial to the induction of flowering. Genes controlling photoperiod response in temperate cereals such as barley (*Hordeum vulgare*) have not been identified previously.

Barley varieties can be broadly classified as winter or spring types. Winter (fall-sown) bar-

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