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Correspondence and requests for material should be addressed to W.G. (e-mail: w.goodwin@formed.gla.ac.uk).

Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest

Kyle E. Harms, S. Joseph Wright, Osvaldo Calderón, Andrés Hernández & Edward Allen Herre

Smithsonian Tropical Research Institute, Apartado 2072, Balboa,
Republic of Panamá

Negative density-dependent recruitment of seedlings, that is, seeds of a given species are less likely to become established seedlings if the density of that species is high, has been proposed to be an important mechanism contributing to the extraordinary diversity of tropical tree communities[1–3] because it can potentially prevent any particular species from usurping all available space, either in close proximity to seed sources or at relatively larger spatial scales[1–18]. However, density-dependent recruitment does not necessarily enhance community diversity[14]. Furthermore, although density-dependent effects have been found at some life stages in some species[3–13], no study has shown that density-dependent recruitment affects community diversity[14,15]. Here we report the results of observations in a lowland, moist forest in the Republic of Panamá in which the species identities of 386,027 seeds that arrived at 200 seed traps were compared with the species identities of 13,068 seedlings that recruited into adjacent plots over a 4-year period. Across the 200 sites, recruit seedling diversity was significantly higher than seed diversity. Part of this difference was explained by interspecies differences in average recruitment success. Even after accounting for these differences, however, negative density-dependent recruitment contributes significantly to the increase in diversity from seeds to seedling recruits.

Here, both within and between species, we link seed input to initial seedling recruitment in the diverse tropical forest on Barro Colorado Island, Panamá (see Methods). With these data, we first estimate the strength of density-dependent recruitment for individual species and show that it is both pervasive and strong across the community. Then, to determine the influence of these effects on diversity, we compare the observed diversity of seedling recruits to (1) the observed diversity of seeds, (2) the expected diversity of seedling recruits after accounting for average differences in recruitment success among species, but in the absence of density dependence, and (3) the expected diversity of seedling recruits after incorporating our species-specific estimates of density dependence. We thereby test the central and previously unexamined issue of whether density-dependent recruitment increases species diversity.

Seedling recruitment was strongly, negatively density-dependent in our 53 focal species (data for *Trichilia tuberculata*, the most common canopy tree at the site, are shown in Fig. 1). Slopes for the seed–recruit regressions were less than 1 for every species, with a median value of just 0.23 (Fig. 2). Nevertheless, high initial seed densities often overwhelmed density-dependent differences in per seed recruitment so that recruit density was greatest where seeds were initially most numerous; regression slopes were weakly positive for 41 of the 53 species (Fig. 2). To determine the net effect on diversity of these potentially conflicting influences, we therefore conducted the following comparisons.

We first compared the observed diversity of seeds with the observed diversity of seedling recruits at each station. Considering only the 53 focal species, the average Shannon–Wiener diversity index was significantly lower for seeds than for recruits (1.33 and 1.95, respectively, paired t-test = 14.7, $P < 0.0001$; Fig. 3a). In addition, the local diversities of seeds and recruits were unrelated

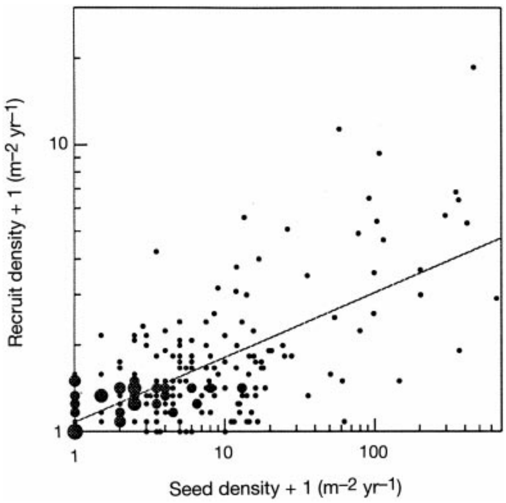

Figure 1 The relationship between the seed density and recruit seedling density for *Trichilia tuberculata* (Meliaceae). The slope of the log–log relationship is less than 1, indicating that recruitment is negatively density dependent. Nonetheless, recruit density increases with seed density. Each symbol represents a census station(s) consisting of one 0.5-m^2 seed trap and three 1-m^2 seedling plots. Symbol size is proportional to the number of stations (ranging from one to six) with identical counts of seeds and recruits.

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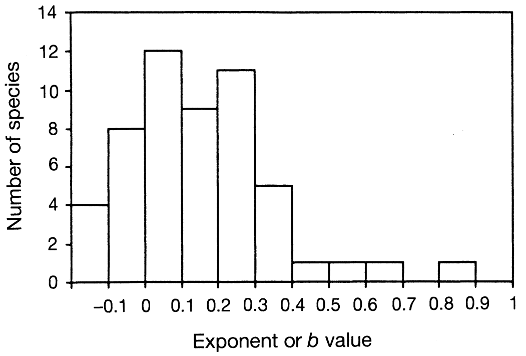

Figure 2 The frequency distribution of the exponent of the relationship between recruit density and seed density for 53 species of shrubs, trees and lianas. All exponents were less than 1 and the median was 0.23, suggesting that strong negative density dependence characterizes seedling recruitment.

(correlation coefficient, $r^2 = 0.0029$); therefore, for these well-sampled species, diversity increased markedly during the seed-to-seedling transition, and the diversity of the local seed rain was a very poor indicator of local seedling diversity. Similarly, the Shannon–Wiener index was lower for the aggregate of all seeds from all stations (2.82) as compared with the aggregate of all recruits (3.80). Moreover, the observed recruit diversity at the 200 stations was very similar to the overall diversity of the 229,071 stems greater than 1-cm diameter at breast height in the 50-Ha plot (Shannon–Wiener index = 3.93)[19].

We then explored the relationship between recruit diversity and seed diversity using species specific, seed-recruit regressions to predict community-level seedling diversity. However, the species-specific regressions incorporate both density dependence and mean seed-to-seedling transition probabilities. In tropical forests, fecund species tend to produce small seeds that require relatively high light intensities to establish successfully, whereas less fecund species tend to produce larger seeds that establish readily in the shaded understory[20,21]. This life-history variation may increase diversity during the seed-to-seedling transition as small-seeded species tend to produce high seed densities and have low seed-to-seedling transition probabilities in the understory. As an example, five species with a seed mass of less than 8 mg accounted for 65.5% of the seed rain but just 5.0% of the recruits in this study. To isolate the consequences of these interspecies differences in average recruitment success, we calculated an expected recruit species composition for each station by multiplying the number of seeds of each species by a species-specific, mean seed-to-seedling transition probability (estimated as mean recruit density divided by mean seed density for each species). The expected diversity of recruits (mean = 1.65) was greater than the observed diversity of seeds (paired *t*-test = 6.92, $P < 0.0001$) but less than the observed diversity of recruits (paired *t*-test = 8.32, $P < 0.0001$; Fig. 3b). Therefore, differences among species in their average success of seedling establishment accounted for part, but not all, of the difference in diversity observed between the seed rain and seedling recruits.

To estimate the influence of species-specific density dependence, we calculated a second expected recruit species composition for each station by substituting the number of seeds of each species into the appropriate, species-specific seed–recruit regression. The expected station diversities incorporating these density-dependent transition probabilities (mean = 1.91) were not significantly different from the observed recruit diversities (paired *t*-test = 1.63, $P > 0.10$; Fig. 3c). Interspecies differences in average recruitment success explained part of the increase in diversity observed during the seed-to-seedling transition. Strong and pervasive density dependence explained the remainder.

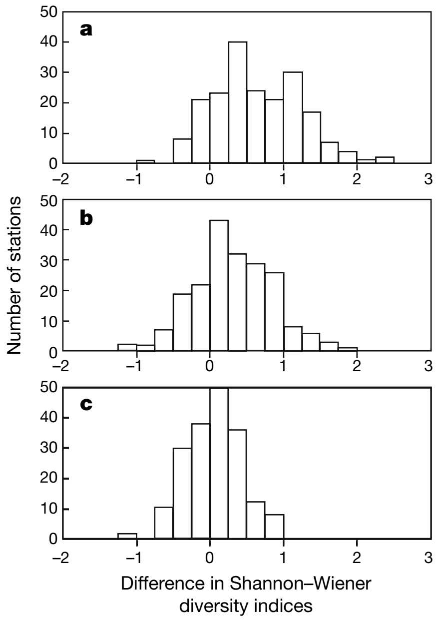

Figure 3 Comparisons of Shannon–Wiener diversity indices within census stations. The diversity of recruits minus the diversity of the seed rain (**a**), the diversity of recruits predicted by incorporating interspecifies variation in average recruitment success (**b**), and the diversity of recruits predicted by incorporating both interspecifies differences in average recruitment success and density dependence (**c**). Predicted recruit diversity converges on observed recruit diversity with the inclusion of species-specific differences in average recruitment success (**b**) and density dependence (**c**).

Several studies have shown high levels of host specificity in herbivorous insects and other pests that consume either leaf or seed tissue of tropical plants; such pests could be involved in producing the observed density-dependent effects[4,7,10,22,23]. Together with our findings, these studies suggest that the high diversity of plant species in this tropical forest is at least partially due to the continuing depredations by the pests and pathogens that selectively kill seeds and seedlings. Moreover, greater pest and pathogen pressure in the tropics[17,24,25], together with the potential effect on plant regeneration shown here, may contribute to the well-known latitudinal gradient in plant diversity. ☐

Methods

Establishing and monitoring census stations

In December 1986, 200 seed traps were erected within the Forest Dynamics Project plot of Barro Colorado Island, Panamá[26,27]. The average distance (±s.d.) between seed traps was 18.9 ± 3.6 m. Each trap consisted of a 0.5-m^2, open-topped, 1-mm wire-mesh bag held 0.8 m above the ground on a PVC frame. All seeds falling into the traps were counted and identified to species each week from 1 January 1987 to 31 December 1998 (ref. 27). Between January and March 1994, all woody plants less than 50 cm tall were tagged and identified to species in 600 1-m^2 plots. These plots were placed 2 m from each of three sides of each seed trap. Survivors were re-measured and new recruits were tagged and identified between January and March each year from 1995 to 1998. Each seed trap and its three adjacent plots constitute a census station.

Over 4 years, the seed rain included 287 species that germinate in soil and averaged 965 seeds $\text{m}^{-2}\,\text{yr}^{-1}$. During the study, most of the 200 census stations never received seeds from most species, in part due to low densities of reproductive adults, variable fecundity and limited seed dispersal[17,27,28]. First-year recruits included 216 species and averaged 5.45 individuals $\text{m}^{-2}\,\text{yr}^{-1}$. Seedling turnover was high, with an average of 55% of a year's recruits dying in their first year.

Regression analyses

To estimate the strength of density dependence on seedling recruitment, we examined the relationship ($R = aS^b$) between the density of recruits (R) and the density of seeds (S). Data were pooled across years within census stations, and care was taken to associate the appropriate years of seed fall and recruitment, especially for species with delayed

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germination. We evaluated the seed–recruit relationship using linear regression of log transformed values of $R + 1$ and $S + 1$ to normalize residuals. In these regressions, the fitted constant b takes values of less than 1 if the per seed probability of recruitment is inversely related to seed density.

Species were excluded from regression analyses if (1) seeds passed through the 1-mm trap mesh, (2) seeds or recruits were recorded at fewer than 10 stations, or (3) seed or recruit density varied less than a factor of four among stations Fifty-three species remained including 28 trees, 20 lianas and five shrubs. These 53 focal species account for 60.3% of the seed rain and 80.4% of recruits. None of the 53 species persist for more than one year in the soil seed bank.

To insure that the regression results were not spurious or artefactual, we conducted several additional tests. First, some traps received many more seeds than could possibly recruit into adjacent seedling plots (simple space limitation). Second, in many instances, seedlings of a given species recruited into some seedling plots, but no seeds of that species were found in the adjacent seed traps. Either or both of these effects would lower b-value estimates and inflate the apparent importance of density dependence. Third, empty stations, lacking both seeds and recruits, introduce an opposing bias, and raise the b-value estimates. To control for the effect of space limitation, we conducted analyses excluding stations in which single species seed densities exceeded the maximum single species recruit density (66 seedlings m^{-2}). To control for the other biases, we conducted analyses after excluding stations lacking conspecific seed. We then eliminated all of these effects by including only stations with non-zero seed densities less than 66 seed m^{-2}. Finally, the addition of 1 before taking logarithms gives b values a downward bias. This effect can be large, particularly when the ratio of seeds to recruits is large. To evaluate the effect of this final potential bias, we compared 95% confidence intervals of the observed b values with b values predicted in the absence of density dependence. Observed b values were significantly less than predicted b values for every species. In all cases, these more conservative tests substantiated the pervasive and strong effects of negative density dependence on seedling recruitment.

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Correspondence and requests for materials should be addressed to S.J.W. (e-mail: wrightj@tivoli.si.edu).

The evolution of syntactic communication

Martin A. Nowak*, **Joshua B. Plotkin*** **& Vincent A. A. Jansen**†

* *Institute for Advanced Study, Princeton, New Jersey 08540, USA*
† *School of Biological Sciences, Royal Holloway, University of London, Egham Surrey, TW20 0EX UK*

Animal communication is typically non-syntactic, which means that signals refer to whole situations[1–7]. Human language is syntactic, and signals consist of discrete components that have their own meaning[8]. Syntax is a prerequisite for taking advantage of combinatorics, that is, "making infinite use of finite means"[9–11]. The vast expressive power of human language would be impossible without syntax, and the transition from non-syntactic to syntactic communication was an essential step in the evolution of human language[12–16]. We aim to understand the evolutionary dynamics of this transition and to analyse how natural selection can guide it. Here we present a model for the population dynamics of language evolution, define the basic reproductive ratio of words and calculate the maximum size of a lexicon. Syntax allows larger repertoires and the possibility to formulate messages that have not been learned beforehand. Nevertheless, according to our model natural selection can only favour the emergence of syntax if the number of required signals exceeds a threshold value. This result might explain why only humans evolved syntactic communication and hence complex language.

The uniqueness of language has been compared to that of the elephant's trunk[13]. Human language is as different from animal communication as the elephant's trunk is from other animals' nostrils. Yet few biologists worry about the evolution of the elephant's trunk (which is a most complex organ that consists of about 6,000 individual muscles and that can perform an unparalleled variety of mechanical tasks), whereas many philosophers, linguists and biologists have great difficulties in imagining how language could have arisen by darwinian evolution[17–21].

A challenge for evolutionary biology, therefore, is to provide a detailed mathematical account of how natural selection can enable the emergence of human language from animal communication. Animal communication is based on three basic designs: a finite repertoire of calls (territorial calls or warning of predators); a continuous analogue signal (for example, the dance of bees); and a series of random variations on a theme (such as the song of birds). All natural animal communication appears to be non-syntactic; some caution, however, seems appropriate as the final verdict on complex vocalization patterns of certain primate species or dolphins has not been reached. In contrast, human language is clearly syntactic: messages consist of components that have their own meaning. We compare non-syntactic and syntactic communication and evaluate their relative performance in an evolutionary setting.

First, we formulate a mathematical model for the population dynamics of language evolution. Suppose a language contains n

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