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PLANT-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Consumer preference for seeds and seedlings of rare species impacts tree diversity at multiple scales

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Abstract Positive density-dependent seed and seedling predation, where herbivores selectively eat seeds or seedlings of common species, is thought to play a major role in creating and maintaining plant community diversity. However, many herbivores and seed predators are known to exhibit preferences for rare foods, which could lead to *negative* density-dependent predation. In this study, we first demonstrate the occurrence of increased predation of locally rare tree species by a widespread group of insular seed and seedling predators, land crabs. We then build computer simulations based on these empirical data to examine the effects of such predation on diversity patterns. Simulations show that herbivore preferences for locally rare species are likely to drive scale-dependent effects on plant community diversity: at small scales these foraging patterns decrease plant community diversity via the selective consumption of rare plant species, while at the landscape level they should increase diversity, at least for short periods, by promoting clustered local dominance of a variety of species. Finally, we compared observed patterns of plant diversity at the site to those obtained via computer simulations, and found that diversity patterns generated under simulations were highly consistent with observed diversity patterns. We posit that preference for rare species by herbivores may be prevalent in low- or moderate-diversity systems, and that these effects may help explain diversity patterns across different spatial scales in such ecosystems.

Keywords Plant–herbivore interactions · Plant diversity · Density dependence · Seed predation · Seedling predation

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Introduction

Understanding the mechanisms that drive and maintain patterns of species diversity in communities is a fundamental aim of ecology (Ricklefs and Schluter 1993; Kreft and Jetz 2007). Plant communities provide an especially tractable system in which to explore the processes that affect diversity. Considerable effort has thus been invested into identifying the factors that create and sustain plant diversity at scales both small (e.g., seed and seedling predation: Janzen 1970; Connell 1971) and large (e.g., landscape-level environmental heterogeneity, dispersal limitation, ecosystem stability, large-scale disturbance: Molino and Sabatier 2001; Condit et al. 2002; Ives and

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Carpenter 2007; Chen et al. 2010). There is also much interest in determining to what extent the drivers of local-scale diversity (i.e., within a given site) also determine emergent patterns of large-scale diversity (i.e., across a landscape) (Schupp 1992; Hubbell et al. 2001; Wright 2002).

One potential driver of plant diversity, first proposed by Janzen (1970) and Connell (1971), is that distinctive patterns of seed and seedling predators are critical to this process. This Janzen–Connell hypothesis posits that consumers often provide critical positive frequency- or density-dependent seed and seedling predation by selectively predating common near-adult individuals of conspecifics; this leads to negative density-dependent survival of species and increased opportunities for rare species, and ultimately engenders increases in local diversity. This tree-scale analysis has been tested extensively in diverse tropical forests and has been scaled up to the level of the forest stand (e.g., Clark and Clark 1984; Carson et al. 2008; Bagchi et al. 2010; Comita et al. 2010; Swamy and Terborgh 2010). These small-scale density-dependent driven changes in diversity are then thought to increase diversity at larger scales (e.g., the level of forested landscape; Harms et al. 2000; Volkov et al. 2005; Adler et al. 2010; Chen et al. 2010). These interactions are widely interpreted as a partial explanation for the maintenance of high-diversity plant communities (Wills et al. 2006; Comita et al. 2010). Much recent work has been directed towards understanding the nuances of how various types of consumers or other "enemies" of regenerating plants, complex trophic interactions, and distance- versus density-dependent predation may work in concert to drive overall positive density-dependent mortality (e.g., Visser et al. 2011; Terborgh 2012).

However, *negative* density-dependent preferences (selective predation of rare food items, leading to positive density-dependent seed or seedling survival) are known to exist across a wide variety of consumer taxa (e.g., Allen and Anderson 1984; Cottam 1985; Smith 1987) and, at least in theoretical models, could lead to very different patterns of diversity (Molofsky et al. 1999). Yet, to our knowledge, there has been no empirical demonstration of the effects of negative density-dependent feeding preferences on diversity patterns. There has also been much less work done on the role of density or density-dependent predation in maintaining patterns of diversity in lower-diversity systems. In the study described in the present paper, which was conducted on a low-diversity tropical atoll (Palmyra), we identified an alternate pathway by which negative density-dependent seed and seedling predation can promote diversity at larger scales (high species turnover across the landscape) precisely because it *reduces* diversity at small (stand-level) scales by causing positive density-dependent survival. We demonstrated the functioning of this pathway in an insular tropical forest, where we found that the dominant herbivores—land crabs—exhibited such strong negative density-dependent patterns of seed and seedling predation. We did this using (1) direct measurements of seed and seedling predation in sites where conspecifics are either common or rare in the canopy, (2) field measurements of tree community diversity analyzed at different scales, and (3) computer simulations of tree diversity at small and large scales, parameterized with field data including selective predation on rare species, which allowed us to project the effects of these patterns over time.

Materials and methods

Study site

This research was conducted in the Palmyra Atoll National Wildlife Refuge (5°53′N, 162°05′W), located in the central Pacific Ocean. The atoll consists of a ring of coral-derived islets surrounding a saltwater lagoon system. The atoll is largely unpopulated, hosting only a small research station on one islet (excluded from this study). As atolls are largely uniform landscapes climatically, topographically, and geologically, they are useful systems in which to investigate how biotic factors drive patterns of community diversity.

Palmyra is almost entirely forested, and has little seasonality in rainfall, temperature, or plant phenology. There are approximately 14 common tree or shrub species on the atoll (see Wester 1985 for a detailed floristic description). The most dominant of these are *Cocos nucifera*, *Pisonia grandis*, *Tournefortia argentea*, *Pandanus fischerianus*, and (at a substantially lower abundance) *Scaevola sericea*. The palm *C. nucifera* (referred to as a "tree" throughout) is by far the most abundant among the common trees and is found in monodominant stands on some of these islets. *P. grandis* and *T. argentea* often form codominant stands, with *S. sericea* also frequently occurring in this forest type. *P. fischerianus* sometimes reaches dominance, but only in small areas of the atoll (Young et al. 2010a). Of these five common tree species, three are small-seeded dicots (*P. grandis*, *T. argentea*, and *S. sericea*), and two are large-seeded monocots (*C. nucifera* and *P. fischerianus*; seed dimensions for each are provided in Table S1 of the "Electronic supplementary material," ESM). Basic natural history information on each of these species, including dispersal mode and density, is provided in "Supplementary Information 1" of the ESM.

The dominant herbivores (and seed predators) in the Palmyra system are land crabs ("Supplementary Information 2" of the ESM). While they undoubtedly also play some role in seed dispersal, at least for short distances, our observations and other work suggest that long-distance seed dispersal is not common ("Supplementary Information 2;" O'Dowd and Lake 1991). The atoll, in part because of its isolation, supports a particularly intact land crab community (land crabs are often hunted on inhabited atolls). There are five common species of land crabs on Palmyra: *Birgus latro*, *Cardisoma carnifex*, *Cardisoma rotondum*, *Coenobita brevimanus*, and *Coenobita perlatus*. All species were present at all survey sites.

Analysis of tree community diversity

Tree communities at Palmyra were surveyed along 50 × 2 m belt transects ($n = 71$; transect dimensions were selected to be consistent with global tropical transect protocols; Phillips and Miller 2002) both on the coast and the interior of islets. Transects were spaced evenly around the coasts of selected islets (2–12 transects per islet), with interior transects laid 50 m inland from coastal transects when the islet was at least 100 m in width (additional sampling details provided in Young et al. 2010a, b). All trees in these transects with diameter at breast height (DBH) $\geq$1.0 cm were identified and measured, and all seedlings <1.0 cm DBH were identified and counted (Young et al. 2010a). We used these transect data to characterize the forest type of an individual transect and to estimate patterns of tree diversity at small and large scales across Palmyra. Small-scale (alpha) diversity was expressed as the mean of the Shannon diversity index (SDI), calculated directly in each of these 71 different transects. Given the very low diversity of species at the site, we supplemented the traditional metric of large-scale, landscape-level diversity—beta diversity—with two additional metrics: (1) coefficient of variation across the SDI values obtained from all of these transects, and (2) a landscape-level clustering metric developed to measure the degree of clustering across a landscape ("Supplementary Information 3" of the ESM). Beta diversity (species turnover) was used rather than gamma diversity (a more typical measure of landscape diversity) because, within this restricted geographic area, the entire system is dominated by the same suite of species.

To create a benchmark against which to judge the observed estimates of small- and large-scale diversity, we compared these empirical tree diversity values against diversity values obtained from randomly generated tree communities. These random tree communities were assembled by populating 71 hypothetical transects (with tree densities that matched observed density values) with random draws from the pooled empirical tree transect data. We then estimated the small-scale (mean SDI) and larger-scale (beta diversity, coefficient of variation of SDI, and landscape clustering metric) diversity in these randomly created datasets. This process was iterated 1,000 times, and data from these iterations were used to build two-tailed probability distributions of both SDI estimates (mean, variance, and coefficient of variation) and plot-based clustering indices. We then compared our field-obtained estimates to these randomly assembled distributions. A highly heterogeneous landscape (high landscape-level diversity), composed of a mosaic of different forest types (low local diversity), would have a lower mean SDI value (local diversity), a higher coefficient of variation of SDI, and a larger clustering index than would be predicted by chance alone. To calculate the statistical significance, each of the various indices were compared against those derived from the 1,000 randomizations using 95 % percentiles; if the mean observed value of the index fell outside the 2.5 and 97.5 % percentiles of the randomizations, the value was significantly different.

As a point of reference to other more typically diverse tropical forest sites that allowed us to further assess the significance of any deviation between the observed and randomly created diversity values at Palmyra and to assess the generality of these patterns in tropical forest systems, we also conducted these same diversity analyses on a body of forest community diversity data collected by A.W. Gentry using similar methods (hereafter "Gentry transects," cf. Gentry 1982) in 21 other widely distributed continental neotropical forest sites ($n = 204$ transects; Phillips and Miller 2002).

Plant–animal interactions in transects

To examine the effects of density of conspecifics on rates of seed and seedling predation, we compared rates of seed and seedling predation across sites with varying abundance of conspecific trees in the canopy. A subset of our vegetation transects ($n = 15$) were used for these experiments. Transect sites were classified as either "*Cocos* forest" ($\geq$90 % individuals were *C. nucifera*; $n = 5$), "dicot forest" ($\geq$90 % individuals were either *P. grandis*, *T. argentea*, or *S. sericea*; $n = 5$), or "*Pandanus* forest" ($\geq$90 % individuals were *P. fischerianus*; $n = 5$). Forests with intermediate densities of palms, *Pandanus*, and mixed dicots were not included in this particular analysis.

Rates of seed predation

To characterize patterns of seed predation, we monitored predation rates on the seeds from the five most abundant tree species in transects where (a) the experimental seed species used was dominant in the canopy and (b) where these seeds belonged to rare species in the canopy. In these transects, we (1) placed seeds in 2 × 2 m plots (seeds per plot: *P. fischerianus* $n = 10$; *C. nucifera* $n = 12$; *T. argentea*, *P. grandis*, and *S. sericea* $n = 20$) and (2) removed any other seeds from within 5 m of these plots in order to enable the identification of seeds used in the study. Up to four plots per transect were used for smaller-seeded species, with each plot separated by a minimum of 15 m (78 plots). Only one plot per site was used for the largest seeded *C. nucifera* ($n = 15$). The number of seeds removed and/or eaten (>50 % seed tissue destroyed) was determined after three days. "Removed" seeds were searched for within 2 m of all directions from the 2 × 2 m plot; the large-seeded species were nearly always relocated, but small-seeded species were frequently not relocated. While it is possible that dispersal is thus confused with predation, observations from Reconyx cameras showed no evidence of crab dispersal of these seeds. For the fleshy *P. fischerianus* it was difficult to accurately assess if consumption of tissue was lethal, so we used relative mass loss across forest type as a proxy for seed predation instead. For a subset of the plots ($n = 18$), seed fate was checked again 30 days and 1 year (*C. nucifera* only) after plot installation to allow time for seeds to germinate. Due to variations in the timing of seed production and seed limitation, *P. grandis* and *C. nucifera* seeds were not placed in the less common *Pandanus* forests. Seeds in *Pandanus* forests were also only monitored for three days. Densities of the seeds (and seedlings) used in this experiment were within the natural range of seed and seedling densities that occur at this site ("Supplementary Information 1" of the ESM). Due to a lack of data normality or homoscedasticity (even after data transformations), Wilcoxon rank-sum tests were used to compare seed removal rates in forest sites where conspecifics were locally rare versus rates in sites where they were locally abundant.

Rates of seedling herbivory

Effects of herbivores on the establishment of experimentally transplanted seedlings across forest types were assessed for the three most abundant tree species (*P. grandis*, *C. nucifera*, and *T. argentea*) in the two most common forest types (dicot forests and *Cocos* forests). For *P. grandis*, seedlings were grown from cuttings; for *C. nucifera* and *T. argentea*, seedlings were collected from the field. When planted (as bare root stock), seedlings of all species were between 3 and 10 cm in height, with at least two healthy leaves and obvious root systems. At this point, seedlings were at a stage when they were likely to be vulnerable to seedling predation.

Seedlings were randomly assigned to one of two treatments: caged ($n = 46$ per species per forest type), or uncaged ($n = 56$ per species per forest type). We used the same ten *Cocos* forest and dicot forest sites used in seed predation trial plots with 8–12 replicates of each treatment at each site. Cage treatments were designed to exclude all medium and large herbivores (i.e., land crabs) and consisted of 0.5 m diameter plots enclosed by 1.2 m high metal mesh (1 × 1 cm openings) buried 20 cm into the ground and rimmed with a 20 cm wide piece of flashing. Cages that were damaged or compromised (e.g., by animal burrowing) were excluded from all analysis ($n = 10$). Uncaged 0.5 m diameter plots allowed all herbivores access to seedlings.

Immediately prior to planting and at every subsequent sampling interval, we measured the number and lengths of all leaves or fronds on each seedling, scored herbivory on each leaf, and used these values to calculate the total leaf area (using established regressions of leaf area, and then subtracting the area removed by herbivores; Young et al. 2010b). Leaf area was assayed in this manner on days 7 (*P. grandis* and *T. argentea* only), 30 (*C. nucifera* only), 60 (*P. grandis* and *C. nucifera* only), 120 (*P. grandis* and *C. nucifera* only), and 365 (*P. grandis* and *C. nucifera* only) of the experiment. *T. argentea* was not monitored after seven days; thus, only acute herbivory responses were recorded for this species. Leaf area across forest type (within species) was compared at 365 days using univariate analysis of variance (ANOVA) with subsequent Tukey HSD analyses (or Wilcoxon tests when the data did not meet assumptions of normality or homoscedasticity). Predation rates were compared using chi-squared tests.

Simulation

We designed a simulation (coded in R) to document what the effects of empirically observed patterns of seed and seedling mortality would be on tree diversity at large and small scales, and to examine if this was consistent with observed patterns of diversity at Palmyra. To do this we created a simulation space of 160,000 square units (1 unit was ~1 m^2 in size) and randomly populated it with individuals of Palmyra's five most abundant tree species (representing 95 % of all individuals measured) at a final density that approached the field-measured tree density (0.15 individuals/m^2). The initial relative abundance of each species was set to be inversely proportional to its seed mass—used as a proxy for dispersal capability (see "Supplementary Information 4" of the ESM). In each generation, we sampled 119 "forest stands" in this simulation landscape, where each stand comprised 100 square units surrounding a randomly selected individual unit (7.5 % of all individual trees). Within each stand we then replaced half of all individuals (randomly selected) within this site with a new "generation" of individuals. The likelihood of the arrival and establishment of a given species in each of these individual units was based on three probabilistic parameters: (1) the dispersal ability of each species (again approximated as the inverse of seed mass; the model was also run with variable dispersal abilities, which yielded similar results in terms of spatial patterns of diversity, see "Supplementary Information 4"), (2) the relative abundance of each species within the randomly selected stand, and (3) the expected lethal mortality rate of each species based on quadratic models of mortality curves as a function of local dominance parameterized using a mortality matrix developed from empirically measured forest-specific seed and seedling predation rates, designed to mimic observed patterns of predation, with higher predation on rare species ("Supplementary Information 4").

A partnered null model was then created using the same simulation, with the sole difference being that we did not weight probabilities of seedling survival by the relative abundance of conspecifics in the stand, thus removing any association between seed/seedling mortality and forest type (including effects of consumer preference for rare species) while retaining idiosyncratic arrival and mortality rates of the species. Analysis of diversity was performed at the point at which the relative abundance of the most dominant species in the density-dependent model approximated that actually observed in the field (6,000 generations). At this point, we randomly designated 71 "transects" in the simulation landscape (size and number of transects mimicked field sampling). We then measured local and landscape-scale diversity levels from these transects using the same metrics employed in quantifying diversity from empirical tree transect data. As with the field data, we then randomly assorted simulated trees across the transects to build random probability distributions, against which we compared diversity patterns derived from the simulation.

Results

Tree diversity at multiple scales

The transect surveys used to empirically measure local-scale diversity at our study site indicated that local diversity was low: 58 % of all transects hosted monodominant tree assemblages (i.e., >90 % dominance of a single tree species), and 20 % were nearly monodominant (i.e., 75–90 % dominance by one species). More than 95 % of all trees sampled were represented by the five most dominant species (see "Study site" above). Comparison of our results to a random empirical distribution obtained by resampling from the actual tree community transects showed that the average field-measured SDI (local diversity; $H' = 0.1825$) was significantly lower than expected by random chance ($P < 0.001$), indicating low local diversity.

Conversely, the landscape-level tree diversity was quite high across the entire atoll. Distributions of common trees were highly skewed, leading to distinct "forest types" at Palmyra ("Fig. S1 of the ESM). Both beta diversity and the observed coefficient of variation of SDI (representative of landscape-level heterogeneity; Fig. 1a) were greater than the values predicted in randomly assembled simulation communities ($P < 0.001$ for both). The clustering metric was also significantly higher than predicted by chance ($P < 0.001$).

Comparisons of small- and large-scale tree diversity at Palmyra to diversity patterns observed in forests elsewhere in the tropics indicated that this lower than random local diversity and higher than random landscape heterogeneity is atypical. Data from Gentry transects surveyed in other tropical forests revealed that the mean of SDI ($H' = 1.215$) and its coefficient of variation (Fig. 1c) were consistent with those expected by random chance ($P = 0.31$ and $P = 0.75$, respectively). While the clustering index for these Gentry transects was higher than predicted by chance ($P < 0.01$), indicating some landscape level clustering, the elevation of clustering above random was only about 30 % as strong as that observed at Palmyra.

Seed and seedling predation

Results from the seed predation trials in the field strongly support the hypothesis that land crabs, the dominant seed and seedling predators at Palmyra, exhibit greatly increased predation on rare species. Predation rates of *C. nucifera* seeds (at one year) were 5.2 times higher in forests where *C. nucifera* formed a minority of the canopy than in forests where *C. nucifera* was dominant ("*Cocos* forests," Table 1). Similarly, average rates of seed removal of small dicot species (after two days; *P. grandis*, *S. sericea*, *T. argentea*) were between 30 and 50 % higher when the seeds were placed in *Cocos*- or *Pandanus*-dominated forests than when they were placed in forests dominated by conspecifics ("dicot forests;" Table 1). The trends persisted over time, although the significance of the difference between seed predation rates varied by species and experimental duration (Table 1). The same patterns appear true for *Pandanus* (Table 1). These early patterns appear to have long-term significance for tree diversity: the only two dicot seed species that survived to become established seedlings did so in dicot forests where conspecifics were dominant in the canopy.

Results from the seedling predation experiments mirrored patterns in the seed predation experiments. Rates of herbivory on *P. grandis* seedlings were considerably lower in conspecific-dominated forests than in *Cocos* forests. Of the 56 *P. grandis* seedlings planted without caging protection in each forest type, 48 % were clipped at base or stripped of all leaf tissue after one day in *Cocos* forests, whereas only 2 % were eaten in this fashion after the same

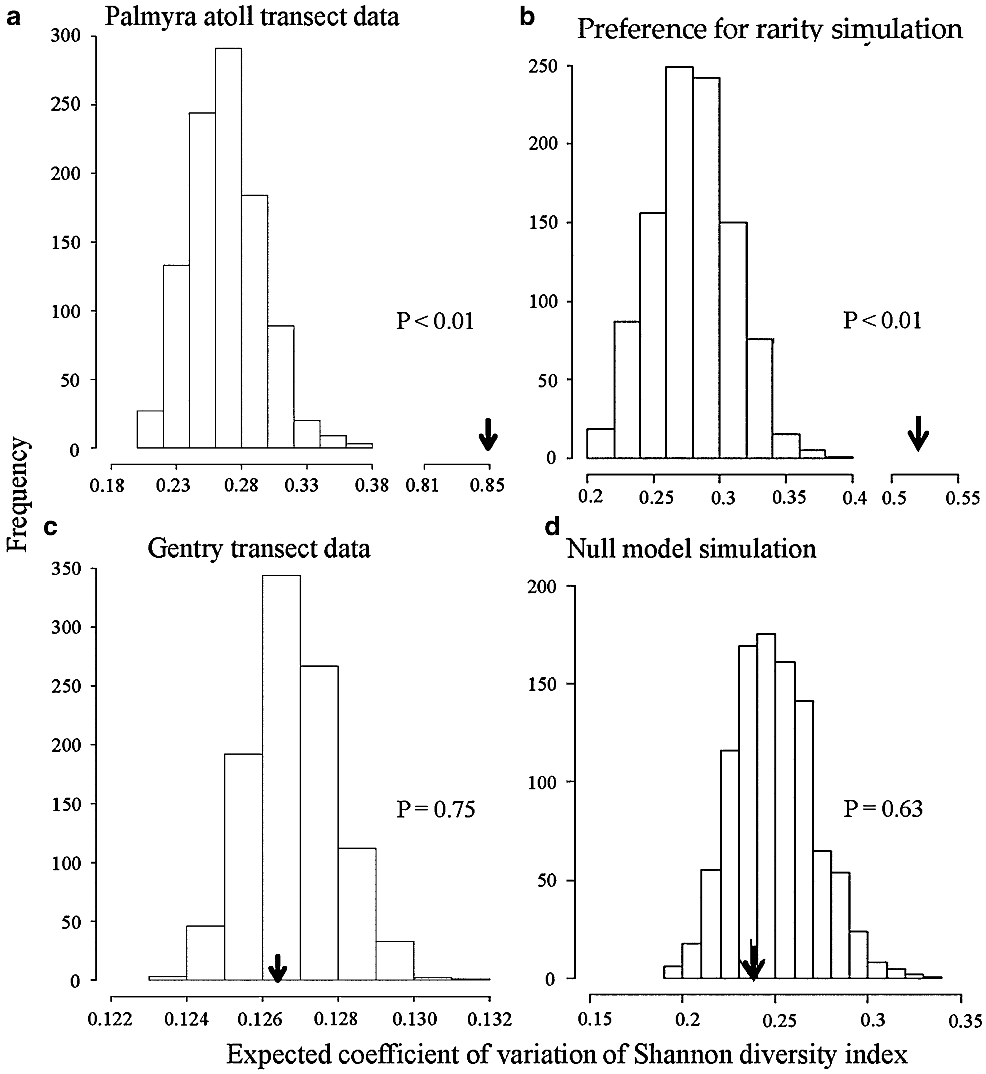


Fig. 1 Observed coefficients of variation of diversity (*black arrow*) in comparison to expected values for **a** empirical diversity data from Palmyra atoll small-scale tree transects, **b** simulated distribution of predation rates ($n = 750$ iterations), **c** external global Gentry transects (204 transects from 21 tropical forest sites), and **d** null model simulation

length of time in dicot forests. After one week, 98 % of *P. grandis* seedlings were missing all leaf tissue in *Cocos* forests, while only 20 % were missing all leaf tissue in dicot forests ($\chi^2 = 16.69$, $P < 0.0001$). In cages that excluded herbivores, there were no missing individuals, mortality was <5 % in either forest type during this first week, and there was no difference in mortality by forest type ($\chi^2 = 2.49$, $P = 0.11$). All of this strongly endorses the hypothesis that herbivory, rather than other site factors, was the principal cause of the seedling mortality we observed. These trends persisted as seedlings matured, as seen in measurements of final leaf area (Fig. 2). At one - year there was significantly lower leaf area for *P. grandis* seedlings in *Cocos* forests as compared to those plants in dicot forests for uncaged plants; in contrast, for caged seedlings of *P. grandis*, there was no significant difference in mean seedling leaf area across forest types (Fig. 2). While rates of predation and nonlethal herbivory on *T. argentea* were only measured at week one, they showed similar patterns to *P. grandis*. Only 38 % of uncaged individuals were eaten after one week in forests dominated by conspecifics, while 53 % were eaten in *Cocos* forests ($\chi^2 = 12.39$, $P = 0.004$). Similarly, when considering leaf area of surviving plants, *T. argentea* in *Cocos* forests also lost significantly more (mean 57 ± 5 %) of their leaf area than when present in dicot forests (mean 32 ± 3 %) after one week ($P < 0.01$, $t = 2.92$, $n = 112$). There was no difference in leaf area lost across forest types for caged *T. argentea* plants ($P = 0.95$, $t = 0.05$, $n = 94$).

The general pattern of increased consumption of locally rare species seen for *C. nucifera* was similar to that observed for *P. grandis* and *T. argentea*. However, rates of

Table 1 Seed predation in different forest types (dominated by *Cocos*, dicots, or *Pandanus*) after two days, one month, and one year (*C. nucifera* only)

Forest type	Species of seed					
	Cocos nucifera	*Pandanus fischerianus*	*Pisonia grandis*	*Scaevola sericea*	*Tournefortia argentea*	All dicots (pooled)
2 days						
Cocos	0	48 ± 1	82 ± 7	85 ± 7	78 ± 7	82 ± 4
Dicot	0	46 ± 1	63 ± 9	62 ± 9	52 ± 9	59 ± 5
Pandanus	–	38 ± 2	–	93 ± 13	78 ± 12	86 ± 8
P (*Z*)	1 (0)	<0.01 (2.8)	0.1 (1.6)	0.08 (1.8)	<0.01 (2.8)	<0.001 (3.7)
1 month						
Cocos	0	–	99 ± 1	100 ± 0	100 ± 0	100 ± 0
Dicot	5 ± 2	–	99 ± 1	93 ± 4	94 ± 5	95 ± 2
P (*Z*)	0.05	–	1 (0)	0.05 (1.9)	0.13 (1.3)	0.03 (2.2)
1 year						
Cocos	14 ± 6	–	–	–	–	–
Dicot	73 ± 16	–	–	–	–	–
P (*Z*)	0.03 (2.2)	–	–	–	–	–

"Dicot" pools data for *P. grandis*, *T. argentea*, and *S. sericea*. Values (mean ± SE) for *Pandanus* only are for % of seed mass removed, rather than % of seeds eaten (all other species). Statistics compare predation levels in sites where conspecifics are locally abundant versus rare in the canopy

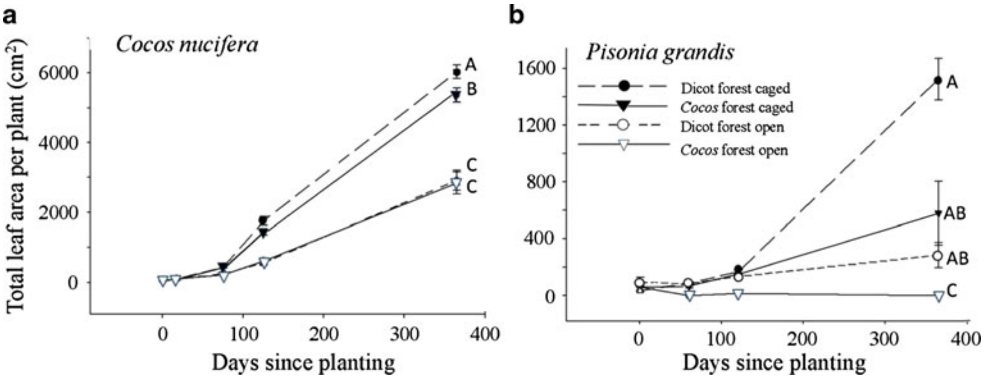
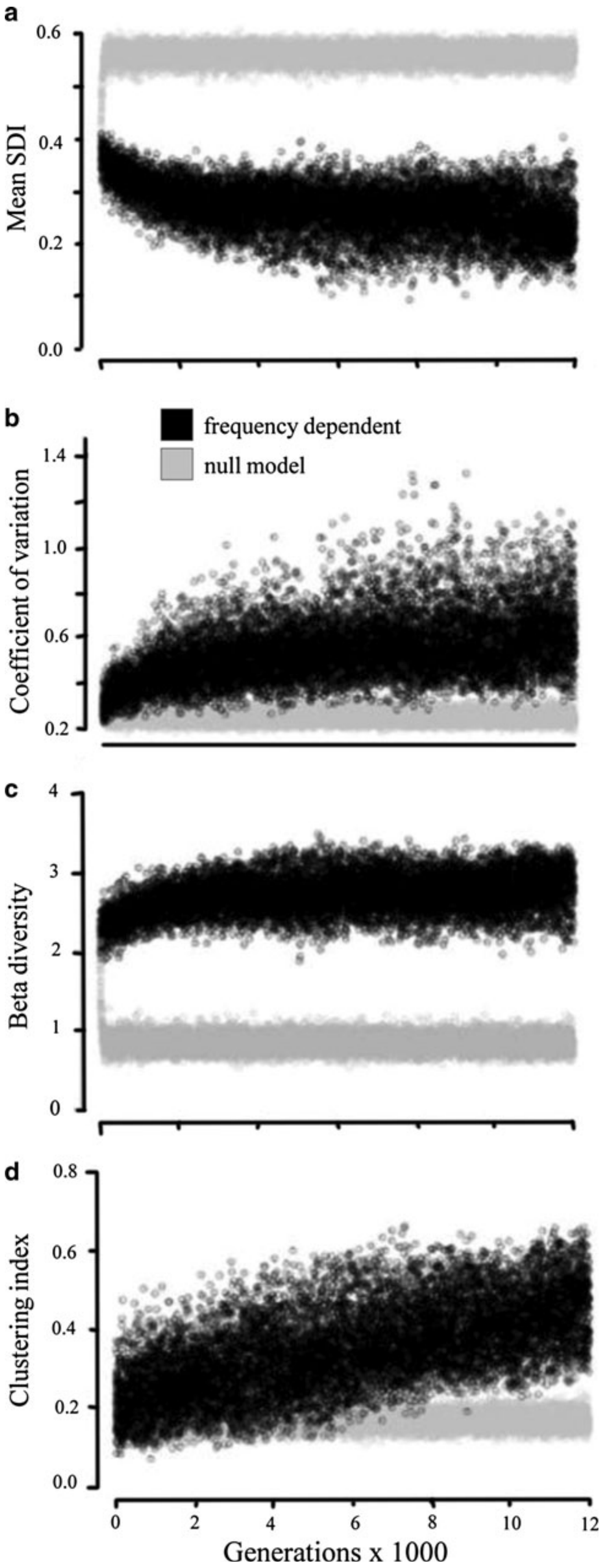


Fig. 2 Average standing leaf area over a one-year period for **a** *Cocos nucifera* and **b** *Pisonia grandis* planted in two forest types, either caged for protection from herbivores or open to herbivores. *Values* show the mean ± SE; *letters* indicate significant differences in leaf area on day 365. Total leaf area of *C. nucifera* in open treatments was essentially identical over time across both forest types, so these lines are overlaid. As no individuals of *P. grandis* survived in *Cocos* forests, there are no error bars

lethal seedling predation on *C. nucifera* were much lower on average than those observed for *P. grandis* or *T. argentea*. Of all the *C. nucifera* seedlings planted without caging protection in each forest type, only 4 % of the seedlings were dead from herbivory after one month (both uncaged plants in dicot forests); after one year, only 13 % of the seedlings were dead from herbivory (again, all uncaged plants in dicot sites; effect of forest type: $\chi^2 = 7$, $P = 0.01$). In contrast to low rates of lethal mortality on *C. nucifera*, there were substantial levels of nonlethal herbivory on dicot plants; leaf area was significantly higher (roughly twice as high) in uncaged plots as caged plots at one year (Fig. 2). While caged plants had greater final leaf area in dicot forests than in *Cocos* forests, uncaged plants performed equally well across forest types (Fig. 2).

Simulation

Of our two simulations, only the first simulation, the "density-dependent predation" simulation, showed similar patterns to those observed in the actual landscape (Figs. S1c, S2a of the ESM). As in the landscape of Palmyra, the local diversity—as measured by the mean SDI ($H' = 0.30$)—in the density-dependent predation landscape was significantly lower than the expected values when individuals were randomly assorted ($P < 0.001$). Likewise, as in the actual landscape, both the observed coefficient of variation of the SDI ($H'_{\mathrm{CV}} = 0.63$; $P < 0.001$; Fig. 1a, b) and the beta diversity ($\beta = 2.86$; Fig. 3c) in the density-dependent predation simulation were significantly higher than expected by chance. By



◀ **Fig. 3** Simulation results for various measures of diversity for a frequency-dependent or null model, including **a** mean Shannon diversity index (SDI), **b** coefficient of variation of SDI, **c** beta diversity, and **d** landscape-based clustering index

contrast, outputs from the null model simulation (lacking increased consumer predation on rare species), including the mean SDI ($H' = 0.56$, $P = 0.882$), coefficients of variation ($H'_{\mathrm{CV}} = 0.24$; $P = 0.642$), and beta diversity ($\beta = 2.86$; $P = 0.33$), did not differ significantly from values that were expected by chance. It is also notable that all of the metrics used to quantify landscape heterogeneity were roughly constant over the 12,000 iterations run in the null model, while in the density-dependent mortalities model, the mean value of SDI decreased nonlinearly with time (Fig. 3a), while the SDI coefficient of variation (Fig. 3b), beta diversity (Fig. 3c), and clustering index (Fig. 3d) increased nonlinearly over time. The Gentry transect data gathered from forest sites external to Palmyra show that this departure from the null model is not typical of other continental tropical forests (Fig. 1c).

Also notable is that results from the density-dependent simulation suggest that *C. nucifera* and *P. fischerianus* will ultimately achieve dominance across the landscape because of the lower overall rates of seed and seedling predation of these species. This does not occur in the null model. However, because of protection for locally dominant species, the ascendancy time to dominance by these two species is very slow in the density-dependent simulation, and after 12,000 iterations these species are still at lower relative abundances than in the null model. Furthermore, density-dependent mortalities permitted the emergence of a spatially patchy forest landscape, even when these two species reach numerical dominance, a large-scale diversity pattern which does not occur in the null model (Fig. S2a of the ESM).

Discussion

When measured at small scales, tree diversity on Palmyra Atoll is extremely low, although the tree species pool at the site is limited. Transect-level estimates of small-scale diversity indicate that forest stands tend to be dominated by just one or two tree species, and have low mean diversities compared to random distributions and to other tropical forest sites. Yet, on a landscape scale there is high heterogeneity in species composition, leading to different forest types, which is revealed when comparisons are made of large-scale diversity across the multiple transects in a landscape.

What maintains this pattern of low local diversity but persistent landscape scale heterogeneity in plant diversity? Dispersal limitation seems unlikely to be driving this patchiness. Among the most dominant species, *P. grandis* disperses on the wings of seabirds that move long distances (Burger 2005), and *C. nucifera* seeds are common in dicot forests and at all coastal sites, regardless of forest type, and disperse readily among islets via water (Young et al. 2010a). There are also no clear differences in topography or parent material in the initially homogeneous atoll environment; however, changes in soil nutrients that develop over time once a given forest type becomes established may entrench monodominance (Young et al. 2010b). But, in the first year of life, caged plants that were protected from herbivores performed the same in sites dominated by conspecifics as they did in sites dominated by other species; caged *C. nucifera* actually performs slightly better in dicot forests (Fig. 2). These points suggest a lack of support for intrinsic site differences as a primary explanation for low local diversity or high landscape heterogeneity. In contrast, there is strong evidence for the role of seed and seedling predators in driving these changes. In the absence of cage protection, *P. grandis* seedlings perform much worse at (and are essentially eliminated from) sites dominated by *C. nucifera*. Likewise, *C. nucifera* seedlings no longer perform better in dicot forests when placed outside of cages and exposed to herbivores. These patterns are similar for seeds as well as seedlings, with all tree species showing higher rates of seed or seedling predation in sites where adults are rare in the canopy. Thus, we are led to conclude that the strong preference for rare species exhibited by the dominant herbivores in this system is likely creating these observed trends. By selectively eating rare seeds and seedlings, these herbivores—counterintuitively—sustain diversity at large scales by promoting low diversity at small scales. However, it is conceivable that differential predation may be only one of multiple drivers causing these patterns; more research is needed to identify consumer preferences as the primary causal agent of diversity patterns observed. Nevertheless, this study only examines two extreme levels of density of conspecifics (where conspecifics are rare, and where conspecifics are common); further studies examining these effects on a gradient of density of conspecifics would help to confirm the patterns observed here.

The effects of selective predation of rare species on local diversity are readily obvious, but the effects on landscape-level diversity may be less intuitive; however, they are well illustrated with examples from this system. Trees that are not currently dominant across the entire atoll (e.g., *P. grandis*) cannot encroach into forests where *C. nucifera* is dominant because of the high rates of seed and seedling predation they face in *Cocos*-dominated forests. Similarly, field data suggest that while *C. nucifera* and *P. fischerianus* can still encroach into dicot forests, as the mortality of these species in dicot forests is not absolute (perhaps due to the larger seed size of these species), selective predation on rare species likely slows their rates of expansion. Thus, negative density-dependent predation promotes and perpetuates landscape diversity by protecting multiple forest types from encroachment of outside species. We suggest the original pattern for this heterogeneity was likely originally created via stochastic processes of establishment. These results are very similar to those predicted by probabilistic cellular automata models, which demonstrate that when the common species always does better, a similar clustering pattern is likely to result, although over very long periods this may ultimately change to monodominance, particularly if there is an imbalance in degrees of consumer selective preferences across species (Molofsky et al. 1999). Consistent with this, longer runs of simulations show similar patterns, but more dominance of preferred species and an eventual loss of more preferred species ("Supplementary Information 5" of the ESM). Such long-term changes to reduced landscape-level diversity may also occur at Palmyra, as only *C. nucifera* appears to be able to encroach into other forest types (Young et al. 2010b).

When the strength of consumer preferences for rare species also varies among plant species, as observed at Palmyra, this will provide a great advantage for less preferred species. The degree of the imbalance in consumer preferences will determine the rates at which diversity at large scales changes. In scenarios where one or few species are considerably more immune to these selective predation patterns, the persistence of large-scale diversity patterns may be ephemeral. At Palmyra, it appears that this advantage, while real, is sufficiently inconsequential that landscape-level diversity is created and maintained for long periods of time. Results suggest that, in simulations that account for the preference for rare species, *C. nucifera* and *P. fischerianus* rise in dominance much more slowly than under a null model of predation, and large-scale diversity is still quite high after 12,000 iterations when selective predation is included (Fig. 3). Likewise, at Palmyra, we are fairly certain that all these species have persisted together for more than 1,000 years (and possibly much longer), despite these strong differential predation patterns, suggesting that these patterns are stable over relatively long time periods (Young et al. 2010a). However, any changes in the initial abundance assumptions (in simulation models) which increase the starting abundance of the less-preferred *C. nucifera* or *P. fischerianus* lead to more limited persistence of locally patchy landscapes, as these less-consumed species can more quickly reach fixation. Thus, the diversity patterns observed likely depend strongly on initial patterns of colonization, which are often difficult to know in real-world environments.

As in many studies of drivers of diversity patterns, our results are based on current diversity data, observed survival patterns, and on simulations integrating these data. Long-term demographic data from this site will be needed to document the ongoing patterns of species change, and to isolate the relative importance of these observed selective predation patterns in creating or maintaining current diversity patterns. Likewise, our current data examines only extremes of rarity (conspecifics <10 %, or conspecifics >90 %); further research will be needed to see if the relationship between frequency of conspecifics and rates of seed and seedling predation is indeed linear.

While there certainly are many low-diversity systems, including tropical systems such as mono-dominated stands of *Mora exelsa* and palm-dominated (*Bactris, Mauritia*) forests, Palmyra's species-poor tree community is not typical of the high-diversity systems we typically think of in the wet tropics. It is thus reasonable to ask if the observed intense selective predation of rare species and its final effects on patterns of diversity are likely to be unique to such low-diversity systems. Other studies conducted in a variety of coastal or insular forests more diverse than Palmyra have shown that land crabs in many island and coastal systems create enormous barriers to the establishment of many plant species, and can thus drive profound declines in local-scale diversity (Green et al. 1997; Sherman 2002; Lindquist and Carroll 2004; Lindquist et al. 2009). There are also numerous other consumers that are known to exhibit negative density-dependent consumption, including rodents (Allen and Anderson 1984), land crabs (Smith 1987; Thacker 1996), birds (Allen and Anderson 1984; Allen and Weale 2004), gastropods (Cottam 1985), and insects (Smith et al. 1989). While it is still unclear what drives these preferences, and patterns may vary based on the overall density of food resources, it seems likely that such a preference may be a strategy employed by consumers to gather rare nutrients (Allen and Anderson 1984; Smith 1987; Thacker 1996). The effects of some of these consumers on small-scale patterns of diversity have been noted in more diverse systems, suggesting that this phenomenon may be widespread (Hassell 1984; Smith 1987; Clarke and Kerrigan 2002). However, both our analyses and those of many others show that the patterns of diversity and of predation we observe are not typical of diverse tropical continental systems (Adler et al. 2010; Chen et al. 2010). It may be that such preferences are only expressed in systems with particular characteristics (i.e., insularity, diversity of species pool), or that certain consumer groups are more likely to exhibit these preferences in the field. Palmyra provided an ideal system in which to identify and examine these patterns, but understanding where and when this apparently common consumer preference for rarity can become prevalent in the landscape and drive patterns of forest diversity will require study across a much broader range of habitats. We believe this will be an important avenue for future research, and may shed new light on how consumers determine the emergent properties of plant community diversity in different ecosystems at various scales.

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