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Seed dispersal increases local species richness and reduces spatial turnover of tropical tree seedlings

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Dispersal is thought to be a key process underlying the high spatial diversity of tropical forests. Just how important dispersal is in structuring plant communities is nevertheless an open question because it is very difficult to isolate dispersal from other processes, and thereby measure its effect. Using a unique situation, the loss of vertebrate seed dispersers on the island of Guam and their presence on the neighboring islands of Saipan and Rota, we quantify the contribution of vertebrate seed dispersal to spatial patterns of diversity of tree seedlings in treefall gaps. The presence of vertebrate seed dispersers approximately doubled seedling species richness within canopy gaps and halved species turnover among gaps. Our study demonstrates that dispersal plays a key role in maintaining local and regional patterns of diversity, and highlights the potential for ongoing declines in vertebrate seed dispersers to profoundly alter tropical forest composition.

biodiversity loss | biotic homogenization | frugivory | mutualisms | tropical conservation

Tropical forests typically have both high numbers of species per unit area and highly variable patterns of community composition through space (1, 2). Dispersal is thought to be a key process underlying this diversity, contributing to high local species richness by allowing the seeds arriving at a site to be drawn from a wide species pool (3, 4) and influencing the spatial arrangement of species by moving seeds away from parent trees, reducing conspecific aggregation (4–8). However, it has proven extremely difficult to quantify the contribution of seed dispersal to local diversity and spatial patterning in forests because it is confounded with other processes, including environmental variation, to which species differentially respond (2, 9); historical legacies, such as past disturbance (10); other biotic interactions, such as competition and predation (11, 12); and stochastic variation (13). Isolating the role of seed dispersal in maintaining diversity in tropical forests has nevertheless taken on new urgency due to widespread declines in populations of vertebrate dispersers throughout tropical regions (14–17). If vertebrate seed dispersal contributes substantially to the diversity and spatial patterning of trees in tropical forests, then declining vertebrate populations could lead to irrevocable changes in forest composition and structure.

To separate the role of dispersal from other processes structuring tree communities, we would ideally manipulate dispersal while keeping other factors constant. For vertebrate dispersal, one approach would be to remove populations of vertebrate dispersers in treatment areas and compare these with untreated areas. However, vertebrate dispersal can occur over long distances (often up to several kilometers) (18), which requires manipulating vertebrate densities over areas larger than is logistically or ethically feasible. To overcome this, studies have used large-scale, unplanned manipulations (19) of vertebrate populations, comparing, for example, the composition of tree communities in areas where vertebrates are heavily hunted with areas where hunting is low (20, 21). Key issues here are that even high hunting pressure has not led to the complete loss of vertebrate dispersers (e.g., ref. 14); hunting also removes vertebrate seed predators and seedling browsers (20, 22, 23), making it difficult to isolate an effect of seed disperser loss alone; and the treatment of interest (removal of vertebrate dispersers) can be confounded with other site differences. Hunting pressure, for example, is often higher in areas without formal conservation protection, meaning these areas experience additional human pressures that affect tree populations, such as forest fragmentation and tree harvesting (14, 20, 24, 25).

Here, we exploit a unique situation, the loss of vertebrate dispersers on the island of Guam (Fig. 1) and their presence on the nearby islands of Saipan and Rota (8, 26, 27), to quantify the contribution of vertebrate seed dispersal to local species richness (alpha diversity) and spatial turnover (beta diversity) of tree seedlings. The three islands have a similar climate and geology; contain native forests of very similar species composition; and originally had a similar composition of vertebrate seed dispersers, comprising only birds and bats with no native vertebrate herbivores. Around 70% of tree species across all three islands have fleshy fruits adapted for dispersal by birds, with no known wind-dispersed species. However, the islands differ in one key respect: Vertebrate seed dispersers (six species of native birds and bats) are now fully or functionally absent from forests on Guam due to predation by the introduced brown tree snake (*Boiga irregularis*) (16, 28), but are present throughout forests on Saipan and Rota (29, 30), which are snake-free. The brown tree snake established on Guam in the 1950s (31), spread across the island, and, by the 1980s, it had eliminated all native bird populations with the exception of one small, isolated population of Micronesian starlings (*Aplonis opaca*) (28). As no nonnative frugivorous birds have replaced those lost, the native forests of Guam are the only place

Significance

Dispersal is considered a key process underlying the high spatial diversity of tropical forests, with the seeds of most tropical tree species dispersed by vertebrates, particularly birds. Although it has proven very difficult to quantify the contribution of dispersal to tree species diversity, it is increasingly important to do so in the face of global declines in vertebrate disperser populations. We show that the complete loss of native seed dispersers on the island of Guam is having a major impact on tree seedling regeneration in canopy gaps, leading to species-poor and spatially aggregated seedling communities. These pronounced changes in patterns of seedling regeneration highlight the importance of dispersal in maintaining patterns of diversity in tropical forests.

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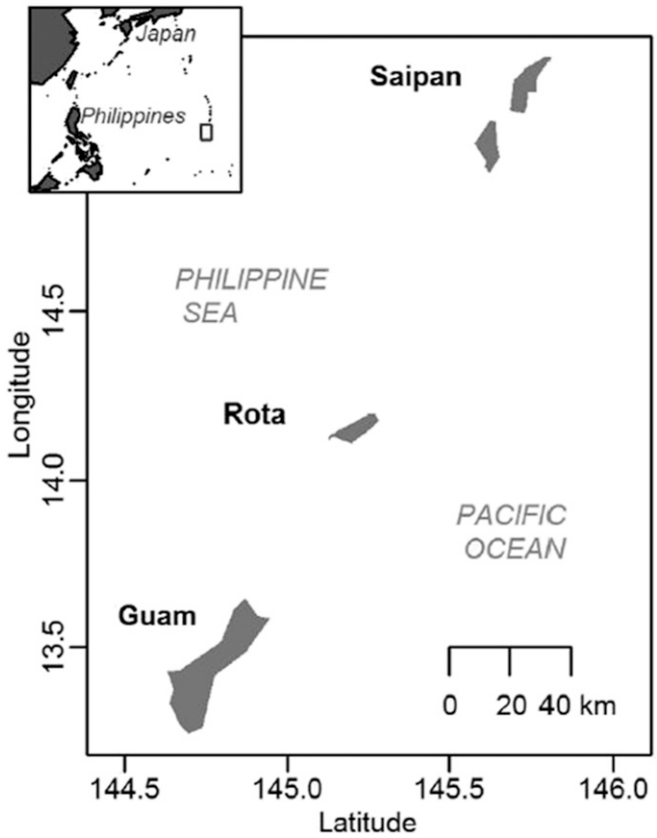

Fig. 1. Map showing the location of the three islands used in this study. Vertebrate dispersers are absent from the southernmost island, Guam, whereas they are still present on Rota and Saipan.

in the world to have lost vertebrate dispersal services (8), providing a unique opportunity to evaluate the role of dispersal in driving spatial patterns of diversity by comparing forest processes on Guam with those on neighboring islands.

Results and Discussion

We focused on the importance of vertebrate dispersal for tree seedling establishment in treefall gaps because the increase in space and light resulting from the loss of a canopy tree is important for the germination and growth of many tree species (32–36), making gaps a key driver of regeneration in tropical forests (32, 37–39). Our aim was to quantify the contribution of vertebrate dispersal to seedling diversity within and among canopy gaps by comparing patterns of gap seedling composition on Guam with those on Saipan and Rota.

We created experimental gaps on each island (15 on Guam, 12 on Saipan, and 8 on Rota) by felling canopy trees, and identified and counted all tree seedlings that had established in each gap 1 y after gap creation (*Materials and Methods*). We allowed a year for seedlings to establish because this incorporated a full growing season to provide an opportunity for most tree species to fruit and disperse their seeds. Performing a census on seedlings after 1 y provides a single snapshot of the regenerating community, which captures patterns of diversity after sufficient time for colonization but before established seedlings begin closing canopy gaps and altering the establishment environment.

We separated seedlings into two categories: (*i*) seedlings that had originated locally via seedfall from adjacent trees and (*ii*) seedlings that had originated from further afield via active dispersal. We classified a seedling as originating locally if it had an adult conspecific surrounding the gap (*Materials and Methods*). We then tested two hypotheses regarding the pattern of local species richness (alpha diversity) across islands. First, we hypothesized that establishment via local seedfall should not be affected by the presence or absence of vertebrate dispersers, such that the relationship between the composition of adult trees immediately surrounding each gap and the seedlings of those species established in gaps should be similar across the three islands. Second, we hypothesized that the presence of vertebrate dispersers on Rota and Saipan should result in a greater total diversity of seedlings in canopy gaps due to additional seed input from further afield via vertebrate dispersal.

Consistent with our first hypothesis, the number of seedling species established in each gap was similar across islands when we considered only seedling species with adult trees surrounding each gap (Fig. 2*A*). For these species, seedling richness per gap increased as surrounding adult richness increased on all three islands (Fig. 2*C*), as would be expected if the tree species surrounding gaps were the source of seedlings within gaps. To more formally assess whether patterns of local seedling establishment differed between islands, and thus whether there might be differences other than the presence or absence of vertebrate dispersers that could confound interisland comparisons, we used the data from Guam to model seedling establishment from local sources only (i.e., considering only those species with an adult tree surrounding each gap), and then tested whether a model describing patterns of local seedling establishment on Guam could account for patterns of local seedling establishment on Rota and Saipan. Our model accounted for differences in adult tree species composition among gaps by assuming that each tree surrounding a gap had a species-specific probability of producing a seedling. These probabilities were estimated using the data from Guam on the number of adult trees of each species surrounding each gap and the number of seedlings of the same

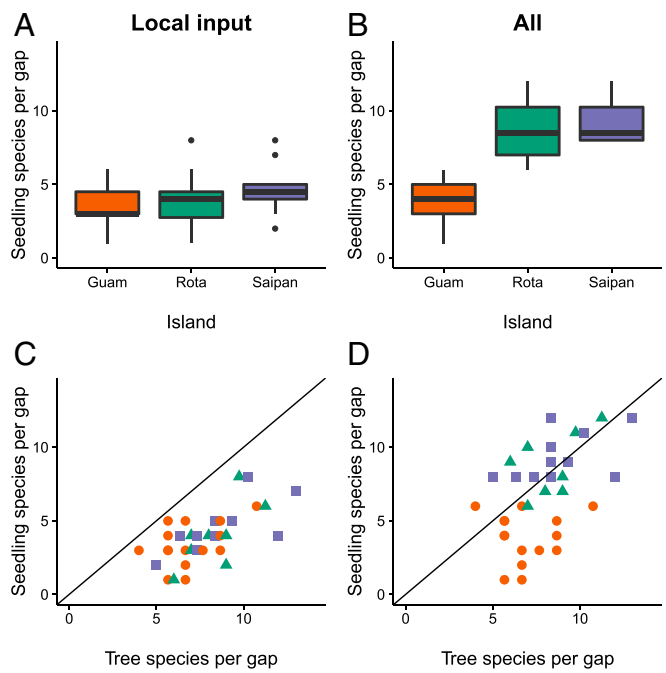

Fig. 2. Gap seedling species richness on an island lacking vertebrate dispersers (Guam) compared with two islands with dispersers (Rota and Saipan). Box plots summarize differences in seedling richness among islands for only those seedlings with an adult tree surrounding the gap (local input) (*A*) and for all seedlings (*B*). Scatter plots show the relationship between seedling and adult species richness at each gap for only seedlings with an adult tree surrounding the gap (*C*) and for all seedlings (*D*) (Guam, red circles; Rota, green triangles; Saipan, purple squares). The black line is a 1:1 line.

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species present in each gap, while simultaneously allowing for differences among gaps in the overall probability of seedling establishment due to differences in gap suitability.

For each island, we used the species-specific probabilities of producing a seedling, estimated from the Guam data, together with data on the adult trees surrounding each gap, to simulate expected gap seedling richness, and we compared simulated with observed outcomes. On Guam, this was a test of model fit, since we compared model simulations with the data used to generate the model. Here, simulated and observed data matched closely, implying the model fitted the data well (Fig. 3 *A* and *B*). On Saipan and Rota, this was a test of whether a model describing patterns of local seedling establishment on Guam could also describe those patterns on Rota and Saipan. Although there was evidence for a slight bias on Saipan, where the model tended to underestimate observed seedling richness, on both Rota and Saipan, discrepancies between simulated and observed data were well within the bounds expected, given uncertainty in the model parameters (Fig. 3 *A* and *B*). These outcomes further confirmed our hypothesis: Patterns of seedling establishment from local seed sources appeared similar across islands, suggesting comparisons were not confounded by strong island-level differences in factors other than vertebrate dispersal.

The data also supported our second hypothesis, that vertebrate dispersal increases local seedling richness (or alpha diversity). Total seedling richness (comprising seedlings originating locally and dispersing from further afield) was consistently higher in gaps on Rota and Saipan relative to Guam (Fig. 2*B*). Our model allowed us to measure the contribution of vertebrate dispersal to local seedling richness by calculating the difference between seedling richness simulated from the model (which assumed seedlings established from local seedfall only) and observed total seedling richness. On Guam, we expected that simulated and total seedling richness would be similar due to the lack of vertebrate dispersers and overwhelming importance of local sources for seedling establishment. This was the case: In 12 of 15 gaps on Guam, the richness simulated by our model matched total richness (Fig. 3*C*), with only three gaps containing seedlings not present as surrounding adult trees. These additional species must have dispersed from beyond the trees surrounding each gap, most likely due to movement by wind or water, or possibly by introduced species like pigs before their exclusion by fencing (*Materials and Methods*). On average, there were 0.45 more species per gap on Guam than expected due to establishment from local seed sources alone (Fig. 3*D*), a difference that could have been due to chance alone, given uncertainty in the model parameters [95% credible interval (CI): −0.20 to 1.13].

We expected the model that assumed dispersal only from local sources would underestimate total seedling richness on Rota and Saipan due to the presence of vertebrate dispersal from further afield, which is what we found (Fig. 3 *C* and *D*). In 15 of 20 gaps, the observed seedling richness exceeded simulated richness by more than would be expected due to model uncertainty (Fig. 3*C*). Furthermore, seedlings lacking a nearby conspecific adult were present in every gap. On average, there were 4.9 more species per gap on Rota (95% CI: 1.9–7.5) and 5.7 more species per gap on Saipan (95% CI: 2.9–8.1) than expected due to establishment from local seed sources alone (Fig. 3*D*). This equated to more than double (2.4-fold) the seedling richness in gaps on Rota and Saipan relative to that expected in the absence of vertebrate dispersers.

Having quantified the contribution of vertebrate seed dispersal to local species richness, we tested a third hypothesis, that seed dispersal decreases species turnover or beta diversity in tropical forests (5). Testing predictions regarding how seed dispersal should influence patterns of seedling species turnover among gaps has proven difficult, since beta diversity varies substantially among forests and at different spatial scales (2, 40). Studies suggest that dispersal should decrease species turnover among sites by moving propagules greater distances and reducing the spatial aggregation of species, leading to less clumped distributions (2, 4, 40), but there have been no empirical tests of this for plants.

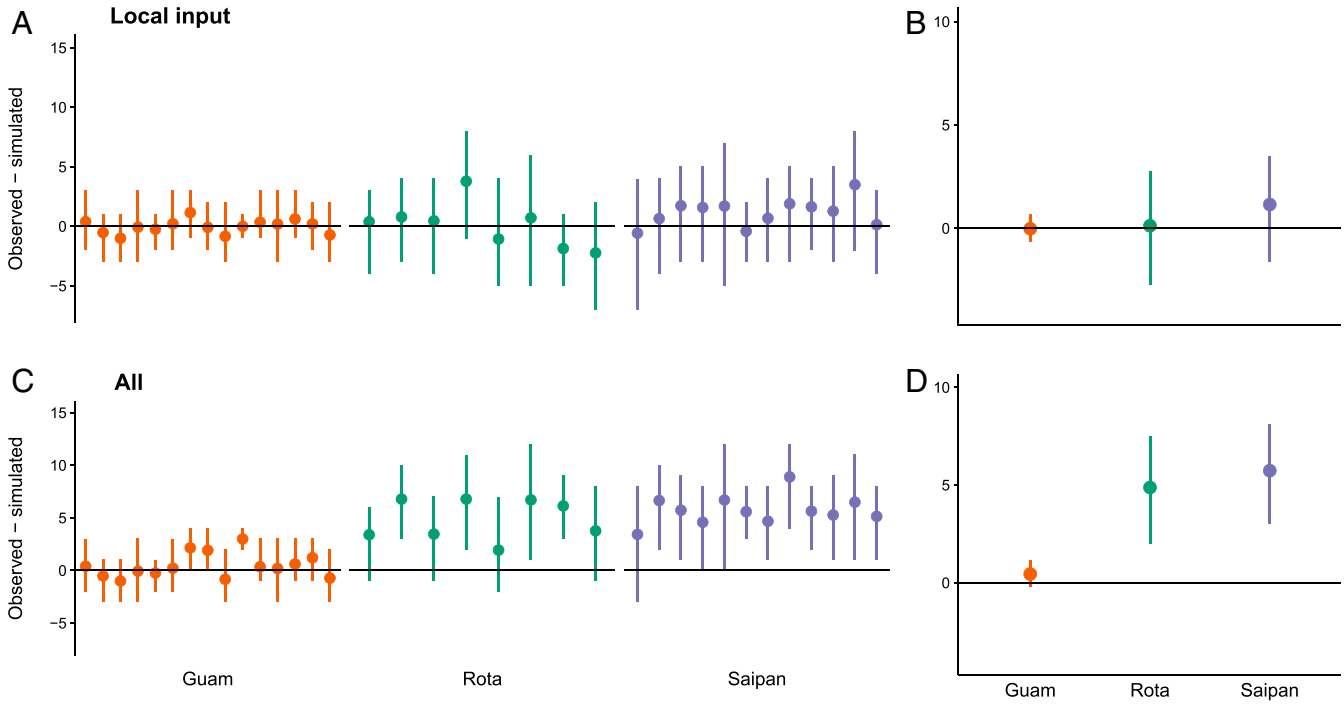

Fig. 3. Observed minus simulated values of gap seedling richness for only those seedlings with an adult tree surrounding the gap (local input) (*A*) and for all seedlings (*C*), as well as overall island means for only those seedlings with an adult tree surrounding the gap (*B*) and for all seedlings (*D*). Bars represent 95% CIs.

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We used the model parameterized on Guam (*Materials and Methods*), which assumed dispersal only from local sources, to simulate the species composition of seedlings in each gap across each of the three islands, based on the composition of the adult community surrounding each gap. The simulated species composition of gaps allowed us to quantify the expected spatial turnover of seedlings among gaps within islands as if seedlings originated from local sources alone, taking into account variation in the composition of adult trees surrounding each gap that could contribute to local seed input (41). For each island, we then compared these simulated beta diversity values with the observed values from the data.

The data supported our hypothesis. On Guam, observed and simulated seedling beta diversity matched closely, while on Rota and Saipan, observed beta diversity was substantially lower than simulated (Fig. 4), indicating that gaps on these islands had a more similar seedling composition than expected due to establishment from local sources alone. These findings show that vertebrate dispersal contributes substantially to species mixing, reducing species aggregation and preventing local seedling communities from being dominated by the adult tree species surrounding each gap. Comparison of observed and simulated values of beta diversity for the seedling community on each island suggests that vertebrate dispersal approximately halved the level of species turnover among gaps (Fig. 4).

Comparing seedling beta diversity with that of the adult tree community surrounding each gap further highlighted just how different the seedling communities were in gaps where dispersers were present (Fig. 4). On Guam, the beta diversity of seedlings was higher than that of adult trees, meaning seedling communities in gaps were more distinct from each other than the adult communities around each gap, most likely because only a subset of adult trees surrounding a gap produced seedlings. On Saipan and Rota, the opposite was true: Seedling communities in gaps were more similar to each other than to surrounding adult communities due to mixing through dispersal. The higher local species richness in gaps on Rota and Saipan was partly attributable to a higher frequency of seedling species that were rarely encountered as adult trees surrounding gaps (Table S1). These species were mostly light-demanding gap specialists, such as *Melanolepis multiglandulosa* and particularly the introduced *Carica papaya*, a fast-growing, light-dependent species. These species also contributed to the lower beta diversity in gaps on Rota and Saipan, since they occurred in almost all gaps on islands with vertebrate dispersers. Thus, dispersal not only increased species mixing, ensuring more species got to more places, but was critical in enabling light-demanding species to reach suitable regeneration sites in canopy gaps (35, 42).

We have documented differences between islands with and without dispersers in their seedling communities 1 y after gap creation, but the long-term consequences of disperser loss for adult tree communities remain to be seen. Critically, we find that light-dependent species are failing to reach gaps where they would otherwise establish if dispersers were present, meaning these species will likely decline in abundance on Guam since they may not persist in mature forest (37). The loss of these light-dependent "pioneer" species could have consequences for gap regeneration processes, particularly if the survival of more shade-tolerant species is dependent on the more moderate light environment pioneers create (34, 35). Moreover, since dispersal away from conspecific adult trees is a way plants can escape the build-up of host-specific pests and pathogens (11, 12, 43, 44), we expect the much stronger association of seedlings with conspecific adults on Guam to increase the exposure of seedlings to pests and pathogens that reduce growth and survival, again affecting gap regeneration.

The loss of vertebrate dispersers from Guam, and their presence on neighboring islands, provides a unique opportunity to isolate the effects of seed dispersal from other factors that underlie diversity patterns in tropical forests. Our findings highlight that global declines in vertebrate populations (14–17) could significantly impact forest regeneration through reducing seed dispersal. While Guam represents an extreme case of complete disperser loss, leading to gap seedling richness being approximately halved and seedling turnover among gaps being doubled, other studies have demonstrated that partial loss of dispersers can reduce seedling diversity and disproportionally alter species abundances (20, 23, 45), particularly of light-demanding pioneer species (22, 46). While we have to wait to see how gap dynamics play out in the presence and absence of dispersers on these islands, our findings show that global vertebrate losses have the potential to profoundly alter tropical forest composition.

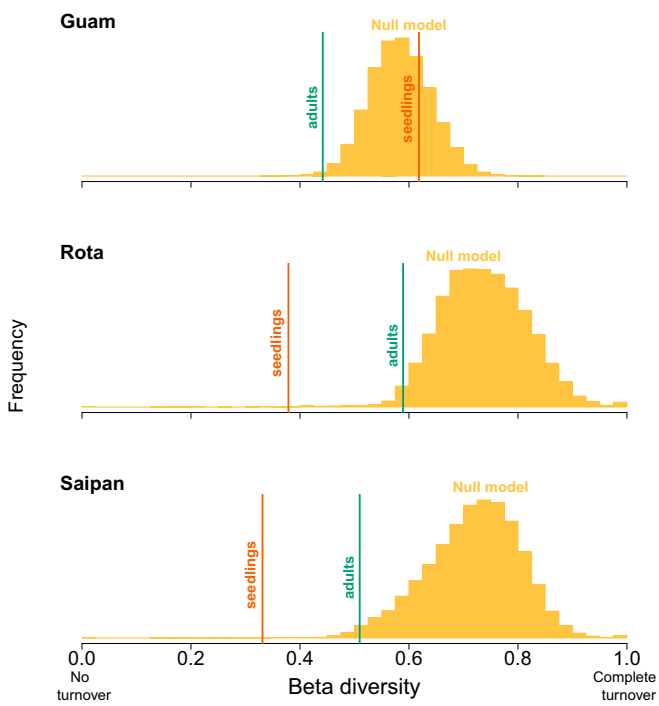

Fig. 4. Posterior distribution of beta diversity for seedlings in gaps on each island assuming establishment from local sources only (null model, yellow bars). The solid red vertical line shows observed beta diversity on each island for all seedlings established in gaps. The solid green vertical line shows observed beta diversity of the adult trees surrounding each gap. Beta diversity was calculated using the Sørensen index of dissimilarity (0 indicates no compositional turnover among gaps, 1 indicates complete turnover).

Materials and Methods

Study Site. The islands of Guam, Saipan, and Rota are part of the Mariana Island chain in the Western Pacific. The islands have a mean annual temperature of around 27 °C with little seasonal variation and pronounced wet and dry seasons. Karst substrate, formed from uplifted corals, underlies much of each island and was originally covered in limestone forest, a moist, broad-leaved evergreen forest, with a low canopy usually less than 11 m tall (47). Patches of natural limestone forest remain on each island; on Saipan, these forests comprise a mixture of 27 canopy tree species with a further 22 understory tree species (48).

Experimental Design. We experimentally created 44 treefall gaps at 11 sites in limestone forest on the three islands: 20 gaps (four at each of five sites) on Guam, 12 gaps (four at each of three sites) on Saipan, and 12 gaps (four at each of three sites) on Rota. One gap at each site on Guam was used for a seed addition experiment, and these five gaps were excluded from this analysis. After gap creation, an invasive slug (*Veronicella cubensis*) consumed most of

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the seedlings in the four gaps at one site on Rota, so we also excluded these gaps from analysis, leaving a total of 35 gaps in this study.

The 11 sites chosen were the locations of permanently marked forest monitoring plots (60 × 60 m) established in 2008–2009. These sites were carefully selected to match forest composition between islands and sample the largest limestone forest remnants on the three islands. Each site is at least 500 m and often several kilometers from other sites on an island.

To locate the four canopy gaps at each site, we started from the midpoint of each permanent plot edge and located the nearest canopy tree outside the plot that was (*i*) one of three common species (*Aglaia mariannensis*, *Cynometra ramiflora*, or *Meiogyne cylindrocarpa*) and (*ii*) located at least 20 m from the edge of any other experimentally created or natural gap. Often, the removal of a single tree was sufficient to create a gap of the desired size; however, in some instances, we removed more than one tree.

During peak fruiting season (July–August), 4 to 6 mo before we created the canopy gaps, we fenced an area corresponding to the canopy projection of each tree (or trees) selected for removal to exclude introduced deer (*Cervus mariannus*) and feral pigs (*Sus scrofa*) from the gaps. Deer are primarily browsers in this system, while pigs are both seed predators and seed dispersers (49, 50). We fenced gaps to remove any confounding effects of differences among islands in the densities of these introduced species, and fences were left in place for the duration of the experiment. In December 2013, we cut down the selected trees and felled smaller trees and branches as required to create gaps with an area of 8–12 m^2, corresponding to the average size of natural canopy gaps in these forests. We estimated gap size from the edge of any vegetation that was at least 2 m tall (51) using the triangle method (52).

To characterize the adult tree community surrounding each gap, we recorded the identity of all adult trees having any part of their canopy within 2 m of the gap edge. We measured seedling communities in each gap 1 y after gap creation in December 2014. To do this, we divided the ground surface beneath each canopy gap into a 0.5 × 0.5-m^2 grid and systematically searched each grid square for seedlings. We identified seedlings to species, except for the genera *Ficus* and *Eugenia*, which each contained two species and whose seedlings are very difficult to distinguish. In addition, because it was difficult to identify small seedlings, we included all seedlings taller than 10 cm for which we were confident of accurate species identification, including any that were present at the time of gap creation (since dispersal events both before and after gap creation may be important). We included all tree and shrub species, regardless of their putative dispersal vector, because we wanted to quantify the contribution of seed dispersal to total seedling richness. Nine species in our study had no obvious adaptations for vertebrate dispersal (Table S1). The majority of these species were recorded infrequently, and rerunning our analysis excluding those species did not change the overall results.

Analysis. To construct a model of seedling establishment from local sources, we used data from Guam on the identity and number of adult trees surrounding each gap (the raw data are provided in Dataset S1), coding each adult species as having a seedling established in the gap (1) or not (0). Seedling species presence or absence was then modeled assuming the outcomes were drawn from a Bernoulli distribution with a different probability (on the logit scale) for each species (reflecting differences among adult tree species in their probability of producing a seedling), each gap (reflecting differences among gaps in their favorability for establishment), and a slope term linked to the number of adult trees of each species surrounding a gap (assuming a greater number of trees of a given species would result in higher seed rain and greater probability of seedling establishment). Differences in establishment probability among species and among gaps were modeled hierarchically, treating these as random effects assuming the probabilities were drawn from normal distributions with means and variances estimated from the data. To allow for potential nonindependence due to similarities among gaps at the same site, we specified a nested hierarchy in which variation among gaps was modeled as drawn from a normal distribution having a different mean for each site, with differences in site means drawn from a normal distribution with mean zero and variance estimated from the data. We fitted the model in a Bayesian framework using the software JAGS v4.2.0 (53), which was run using the package jagsUI (54) in R v3.1.1 (55) (the full model is provided in Dataset S2). We included noninformative priors for the overall probability of an adult species producing a seedling and for the slope of the relationship between the number of adult trees and seedling probability, specifying these as having mean zero and variance 25 on the logit scale, and noninformative priors for all variance terms, specifying these as having uniform priors for the SD in the range from 0–10. We obtained posterior distributions of parameters by running the model with three Markov chain Monte Carlo (MCMC) chains for 40,000 iterations after a burn-in of 10,000 iterations. We checked the model for convergence by examining the trace plots and calculating the Gelman–Rubin statistic, with all monitored parameters having values less than 1.1, implying adequate convergence (56).

To assess the fit of the model to the data from Guam, we carried out a posterior predictive check by simulating data from the model and comparing the observed data with simulated outcomes (57). We simulated seedling presence or absence for each adult species surrounding each gap using the parameters from the fitted model at each iteration of the MCMC chains and calculated seedling richness by summing these presences. This produced 120,000 simulations (40,000 iterations by three chains) of seedling richness for each gap: We used the mean difference between observed and simulated values of gap seedling richness, and associated 95% CIs, to measure how well the model fitted the data. We then used the model developed on Guam to simulate seedling richness on Rota and Saipan. Here, the simulations were compared with independent data not used in model construction, providing a strong test of the prediction that the processes underlying seedling establishment from local sources on Guam were similar on Rota and Saipan.

Each of our simulations provided a list of the simulated seedling species in each gap based on the probability of adult trees surrounding each gap producing a seedling. We used these simulated seedling communities to calculate the seedling turnover among gaps (beta diversity) that would be expected, given establishment from local sources alone. We used the Sørensen index to measure beta diversity, as recommended to measure differences among communities (58), calculating the average pairwise dissimilarity among gaps using the binary variant of the Bray–Curtis index (equivalent to the Sørensen index) as implemented in the vegan v2.4-0 (59) package in R. The index takes values between 0 (all seedling species are present in all gaps, meaning no compositional turnover) and 1 (every gap contains unique seedling species, meaning complete compositional turnover from one gap to the next). We compared simulated values of beta diversity with the observed values on each island.

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