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Long-term research impacts on seedling community structure and composition in a permanent forest plot

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Abstract

Long-term ecological research projects have become cornerstones for the study of forest dynamics worldwide. The intense, large-scale research efforts necessary to monitor ecological processes may alter natural processes and be a source of error in analyses. This study evaluated whether trampling due to concentrated researcher presence has altered the structure and composition of the seedling layer in the 50 ha permanent sample plot on Barro Colorado Island (BCI), Panama. Since 1980, major research projects in the plot have included complete tree censuses every 5 years, weekly seed trap collection, and the more recent annual censuses of 20,000 1 m^2 seedling quadrats. We compared data from these pre-existing seedling quadrats with data from 600 newly established seedling quadrats in an area of much lower research intensity adjacent to the 50 ha plot and tested for differences in seedling density, height-class distributions, species richness and composition. Although we expected to find evidence of researcher impacts on the seedling layer, we found no significant differences in seedling community structure or composition inside and outside of the BCI 50 ha plot. We conclude that there is no evidence that research efforts within the BCI plot have thus far resulted in significant changes in the seedling layer. The extent of research impacts is likely to differ under varying environmental conditions and research protocols. Continued efforts should be made to quantify the impacts of research methodology at long-term research sites in order to detect site-specific or long-term changes.

Keywords: Disturbance; Forest dynamics plot; Long-term ecological research; Research impact; Seedling community; Tropical forest

1. Introduction

Long-term ecological research sites have become fundamental tools in the study of community and ecosystem dynamics in forests worldwide (Condit, 1995; Sheil, 1995; Hobbie, 2003). Studies at these sites generate data on ecological processes across multiple spatial and temporal scales, providing insights into various aspects of ecosystem functioning, such as disturbance dynamics, species coexistence, climate change, and biogeochemical cycling (Hobbie et al., 2003). Most long-term vegetation studies are non-manipulative by design, but this does not preclude unintended or accidental impacts associated with researcher activities that may alter vegetation dynamics and result in biased data (Sheil, 1995; Malhi et al., 2002; Phillips et al., 2002). Therefore, to insure the validity of conclusions based upon long-term research, it is essential to quantify the potential impacts of researcher presence and activity on the dynamics being studied.

This study was designed to assess whether long-term, high intensity research activity alters seedling dynamics in a 50 ha permanent sample plot on Barro Colorado Island (BCI), Panama. The primary research objective of the BCI plot, which was established in 1980, is to collect long-term, spatially explicit data on tropical tree dynamics in order to advance scientific understanding of the maintenance of tropical plant diversity (Hubbell and Foster, 1983). All free-standing, woody stems $\geq$1 cm DBH in the BCI plot have been measured, identified, and mapped at 5 year intervals, totaling approximately 214,000 stems of over 300 species (Hubbell and Foster, 1983). Each census requires 14–16 field assistants working for

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9 months, an estimated 53 person-days ha^{-1} (Condit, 1998). In addition to the primary tree census, many other projects that range in scope and magnitude are conducted in the BCI plot, including several long-term efforts. An annual census of canopy structure in each 5 m × 5 m section of the plot was initiated in 1983 (Hubbell and Foster, 1986a). In 1985, 60 litter traps were established for weekly collection, and 200 seed traps followed in 1987 (Dalling et al., 2002; Wright et al., 2004). In 1994, 600 seedling quadrats were established for an annual census (Harms et al., 2000). The most recent large-scale project in the BCI plot began in 2001 and involves annual censuses of seedlings and small saplings in 20,000 1 m^2 quadrats distributed throughout the 50 ha plot.

Although research in the BCI plot is limited primarily to non-destructive sampling and measurements, with restrictions against collections and manipulations, the high volume of research activity in the plot has been a source of concern. Researchers walking through the BCI plot on a regular basis may trample and injure or kill seedlings, particularly of more vulnerable species, resulting in shifts in the structure and composition of the seedling layer. To test for such researcher impacts, we compared seedlings in quadrats located inside and outside of the BCI 50 ha plot. We expected the higher foot traffic inside of the BCI plot to result in lower seedling densities compared to outside of the plot. Since smaller seedlings tend to be more vulnerable to physical damage (Clark and Clark, 1991), we also predicted differences in size class distributions, with fewer individuals in smaller height classes inside the BCI plot compared to outside.

Disturbance associated with long-term research may also promote changes in species composition (Denslow, 1996). Thus, we tested for differences in species richness and for shifts in the relative abundances of the most common species inside and outside the BCI plot. We also tested for differences in relative abundance of growth forms, as growth forms such as lianas may exploit microhabitats created by disturbances similar to human trampling (Schnitzer and Bongers, 2002).

The large-scale seedling census initiated in 2001 requires that a researcher stand or kneel adjacent to each 1 m^2 seedling quadrat for up to 30 min in order to measure, tag, and map all seedlings. This may negatively impact seedling survival in the area immediately surrounding each quadrat, artificially reducing seedling competition and benefiting seedlings located inside the quadrat. To test for this localized effect of researcher presence, we compared seedling density in quadrats located inside the BCI plot to the density of seedlings in the area immediately surrounding the associated seedling quadrats. We expected that these adjacent areas would have lower stem density compared to their associated seedling quadrats.

2. Methods

We conducted the study on Barro Colorado Island, Panama (9°9′N, 79°51′W), a 1500 ha former hilltop that became an island in artificial Gatún Lake when the Chagres River was dammed in 1914. The island was declared a reserve in 1923, at which time it was already the site of floral and faunal studies (Leigh, 1999). In 1946, BCI was placed under the jurisdiction of the Smithsonian Institution, which has maintained an active research station on the island since the 1960s (Leigh, 1999).

BCI supports old growth and secondary moist tropical forest with an annual rainfall of 2600 mm and a mean annual temperature of 27 °C (Dietrich et al., 1992). The 50 ha permanent forest dynamics plot is located on the island's central plateau 128–155 m above sea level and sits on an andesite flow composed of well-weathered oxisols. Forty-eight of the 50 ha consists of old growth forest, which has experienced minimal human disturbance for at least 500 years. The remaining 2 ha were subject to clearing in 1900 (Piperno, 1990). Researchers access projects within the 50 ha plot by means of approximately 3 km of well-used trails running through the plot. Trails are generally between 0.5 and 1.0 m wide, and thus cover less than 0.6% of the total area of the plot (Comita et al., unpublished data).

To test for differences in the composition of woody seedlings generated by human traffic, we established 600 1 m^2 control seedling quadrats at 5 m intervals around the plot at a perpendicular distance of 20 m from the nearest edge of the 50 ha plot. We compared data on seedlings in these control quadrats to data from 20,000 existing 1 m^2 seedling quadrats located at 5 m intervals inside the 50 ha plot. Some research is conducted in the forest adjacent to the 50 ha plot; however, research activity is much more concentrated in the plot and researchers conducting long-term projects in the 50 ha plot generally remain within the boundaries of the plot when collecting data. In each control quadrat, we measured the height and identified to species all free-standing, woody stems $\geq$20 cm tall and $<$1 cm DBH, identical to the methods used in the census of seedlings in the 20,000 quadrats in the BCI 50 ha plot. All tagging and measuring was conducted in June and July 2004, with subsequent species identification in October and November 2004. Between sampling and identification, 63 seedlings died, while 71 additional seedlings could not be identified. Data from seedling quadrats outside the 50 ha plot that were within 2 m of a trail or were noticeably impacted by nearby research were discarded (14 plots), leaving 586 seedling plots for use in statistical comparisons. Data from existing 1 m^2 seedling quadrats inside the 50 ha plot were collected between January and July 2004. Five hundred thirty-nine of the 20,000 plots located inside of the 50 ha plot were not censused in 2004 to avoid damaging nearby ongoing research projects.

To test for differences in seedling density inside and outside of the BCI 50 ha plot, we used resampling techniques to generate 95% confidence intervals around the mean density of seedlings inside of the 50 ha plot. To account for differences in sample size and to be consistent with the sampling scheme used outside of the 50 ha plot, the sampling distribution of the mean inside the plot was determined by randomly drawing 2 *x*-coordinates and 2 *y*-coordinates, pulling the 200 seedling quadrats falling along each of the *x*-coordinates (running east–west, 400 total plots) and the 100 quadrats falling along each of the *y*-coordinates (running north–south, 200 total plots).

Five hundred ninety-six unique quadrats were pulled in total, since the x and y lines cross in four places. This procedure was repeated 1000 times with replacement, and 95% confidence intervals were generated from the 25th and 975th ranked values of mean seedling density. Seedling density was considered significantly different inside versus outside of the 50 ha plot if the mean density of seedlings in quadrats outside of the 50 ha plot fell outside of the 95% confidence intervals generated by resampling quadrats from inside the plot.

To determine the power of our analysis to detect a difference in seedling density between inside and outside the 50 ha plot, we calculated the ratio of density inside the plot to density outside the plot in 1000 bootstrapped samples. For each of the 1000 bootstrap replicates, we separately resampled quadrats from inside and outside the plot with replacement, calculated mean seedling density for each sample, and then divided the mean density inside by the mean density outside the plot. As described above, quadrats inside the plot were resampled in such a way as to mimic the sampling scheme used outside the plot. The 25th and 975th ranked values of the ratio of density inside to density outside correspond to the values for which a significant difference is detected at the $\alpha = 0.05$ level, while the 5th and 995th ranked values correspond to a significant difference at the $\alpha = 0.01$ level.

We tested for differences in height-class distribution, species richness, and relative abundances of both growth forms and common species inside and outside the 50 ha plot using resampling techniques similar to those used to test for a difference in seedling density. To test for differences in height-class distribution, seedlings were divided into seven height-classes: 200–249; 250–299; 300–399; 400–599; 600–999; 1000–1999; and 2000–3000 mm. We compared the density of stems in each height-class outside of the 50 ha plot to the 95% confidence intervals generated around the mean density of stems in each height-class inside of the 50 ha plot. To test for differences in species richness, we compared the total number of species identified in quadrats outside of the 50 ha plot to the 95% confidence intervals around the total number of species in quadrats sampled from inside the 50 ha plot. To test for differences in growth form, we assigned all individuals to one of five categories based on maximum adult height and growth pattern: shrubs (<4 m tall), understory trees (4–10 m), midstory trees (10–20 m), canopy trees (>20 m), and lianas (climbing woody vines) (Hubbell and Foster, 1986b). We compared the proportion of stems in each growth form outside of the 50 ha plot to the 95% confidence intervals around the proportion of stems in each growth form inside the 50 ha plot. To test for differences in the relative abundances of common species, we compared the relative abundances of the 10 most common species outside of the 50 ha plot to the 95% confidence intervals around the relative abundance of each of the 10 most common species in quadrats sampled from inside of the 50 ha plot.

To test for localized effects of researchers on seedlings adjacent to seedling quadrats, we quantified seedling density in the areas immediately surrounding 90 1 m^2 seedling quadrats located inside the 50 ha plot. We counted seedlings within 0.5 m of the edge of seedling quadrat on two sides of the quadrat. For each seedling quadrat, we calculated the difference in seedling density (m^{-2}) between inside and adjacent to the quadrat. To test whether the difference in seedling density between inside and adjacent to the seedling quadrats was significantly different from zero, we generated 95% confidence intervals around the mean difference (density inside − density adjacent) by resampling the vector of differences 1000 times with replacement (i.e. bootstrapping). All analyses were performed using R Statistical Package 2.1.0 (R Development Core Team, 2005).

3. Results

There were 1539 free-standing woody seedlings in the 586 1 m^2 quadrats outside the BCI 50 ha plot, whereas inside of 50 ha plot we counted 60,620 seedlings in 19,461 seedling quadrats included in the 2004 census. Seedling densities inside and outside of the 50-plot were not significantly different. Mean seedling density outside the plot (2.63 ± 0.13 S.E. seedlings/m^2) was within the 95% confidence intervals generated for seedling density inside the plot (2.41–3.65 seedlings/m^2; Fig. 1). Any difference in the ratio of seedling density inside the plot to seedling density outside the plot is likely to fall between 0.94 and 1.48 at the $\alpha = 0.05$ level, and between 0.90 and 1.60 at the $\alpha = 0.01$ level. Thus, we can confidently exclude the result that trampling caused a >10% reduction in seedling density inside the plot. We also found no evidence of differences in height-class distribution inside and outside of the 50 ha plot. The mean densities of seedlings in respective height-classes outside the plot were all within the 95% confidence intervals generated around height-class densities inside the plot (Table 1).

We identified 163 species among 1399 seedlings outside of the 50 ha plot and 341 species in the pre-existing seedling quadrats inside the plot. Accounting for differences in sample sizes using resampling techniques, the total number of species

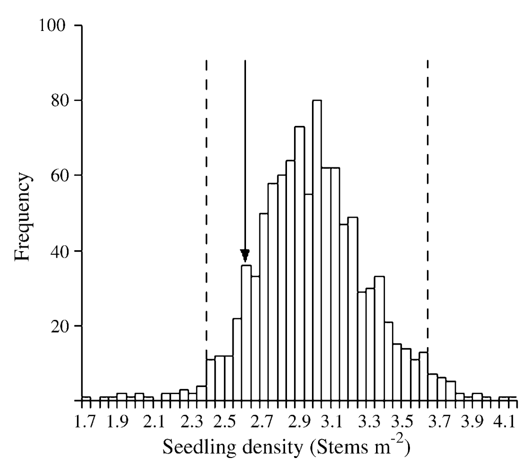

Fig. 1. Histogram of mean seedling density (m^{-2}) in each of 1000 random draws of 596 seedling plots located inside the permanent 50 ha plot on Barro Colorado Island, Panama. Dashed lines represent 95% confidence intervals. Arrow represents the mean seedling density of 586 seedling quadrats located outside of the 50 ha plot.

Table 1
Density of seedlings in each height-class inside and outside of the BCI 50 ha plot

Height-class (mm)	Seedling density (m^{-2})		
	Outside	Inside	Inside 95% confidence intervals
200–249	0.59	0.60	0.45–0.77
250–299	0.41	0.48	0.36–0.62
300–399	0.50	0.57	0.44–0.71
400–599	0.45	0.52	0.39–0.65
600–999	0.35	0.35	0.27–0.43
1000–1999	0.27	0.24	0.19–0.29
2000–3000	0.06	0.06	0.04–0.08

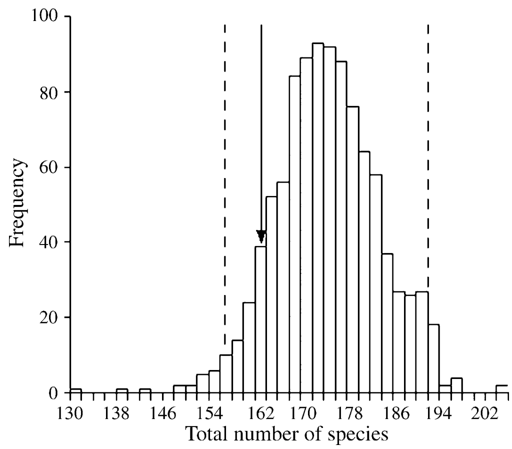

Fig. 2. Histogram of the total number of species in each of 1000 random draws of 596 seedling plots located inside the 50 ha plot on Barro Colorado Island, Panama. Dashed lines represent 95% confidence intervals. Arrow represents the total number of species identified in a sample of 1399 individuals in seedling quadrats located outside of the 50 ha plot.

outside the plot was within the 95% confidence intervals around the number of species inside the plot (157–192 species; Fig. 2), indicating that species richness does not differ significantly inside and outside the 50 ha plot.

We also found no significant differences in seedling community composition inside and outside of the BCI 50 ha plot. There were no significant differences in the proportion of individuals in each growth form outside compared to inside of the 50 ha plot (Table 2), or in the relative abundances of the 10 most common species inside and outside of plot (Table 3). Seven species were among the 10 most abundant species both inside and outside the 50 ha plot. Of the 163 species identified in seedling quadrats outside the 50 ha plot, 157 were also found inside the plot, indicating that the species found outside of the plot are largely a subset of the species inside the plot.

Table 2
Proportion of seedlings assigned to each growth form inside and outside of the BCI 50 ha plot

Growth form	Proportion of stems		
	Outside	Inside	Inside 95% confidence intervals
Lianas	0.20	0.20	0.17–0.23
Shrubs	0.21	0.21	0.17–0.25
Understory trees	0.14	0.16	0.14–0.19
Midstory trees	0.12	0.12	0.10–0.15
Canopy trees	0.33	0.30	0.25–0.37

Table 3
Relative abundance of the 10 most common species in the seedling layer inside and outside of the BCI 50 ha plot

Relative abundance rank	Proportion of stems		
	Outside	Inside	Inside 95% confidence intervals
1	0.063	0.064	0.059–0.125
2	0.059	0.063	0.050–0.077
3	0.058	0.048	0.041–0.068
4	0.048	0.043	0.037–0.059
5	0.034	0.042	0.033–0.050
6	0.034	0.040	0.030–0.045
7	0.032	0.036	0.026–0.040
8	0.027	0.031	0.023–0.036
9	0.023	0.025	0.021–0.032
10	0.021	0.024	0.020–0.029

We also found no evidence of localized researcher impact on seedling densities in the areas immediately surrounding the seedling quadrats within the 50 ha plot. Mean seedling density in areas immediately surrounding seedling quadrats in the 50 ha plot was 2.27 seedlings/m^2 (0.28 S.E.) compared to a mean of 2.79 seedlings/m^2 (0.34 S.E.) within the corresponding seedling quadrats. The bootstrapped 95% confidence intervals around the difference in seedling density inside and adjacent to seedling quadrats overlapped zero (−0.152 to 1.244), indicating no significant difference between the two areas.

4. Discussion

Following 25 years of concentrated research, we found no significant differences in seedling community structure and composition inside the BCI 50 ha plot compared to adjacent areas experiencing lower research intensity. Although we expected that mortality associated with researcher activity would lower seedling density and the number of seedlings in smaller height classes, we found no differences between seedling densities or height-class distributions inside and outside the 50 ha plot. Most surprising of all, we found no evidence of a localized researcher effect on seedling density in areas immediately surrounding seedling quadrats inside the 50 ha plot. Conscious efforts by field assistants to avoid damaging seedlings in adjacent areas when censusing seedling quadrats may have mitigated localized trampling impacts.

If researchers also actively avoided marked seedlings within quadrats when walking through the study area, our estimates of seedling density inside the BCI 50 ha plot could be artificially inflated. However, mean seedling density in the quadrats inside the 50 ha plot changed little between when seedling quadrats were first marked in 2001 and when we made the comparison between seedling densities inside and outside of the 50 ha plot in 2004 (Comita & Hubbell, unpublished data). Thus, seedlings within marked quadrats are not afforded any protection that would lead to biased estimates of seedling density inside of the 50 ha plot.

We also expected human trampling to induce changes in species diversity and composition; however, there were no significant differences in species richness or community composition inside and outside the 50 ha plot. The six species found outside, but not inside, the 50 ha plot likely represents a sampling effect, since a large number of BCI species are rare (Hubbell and Foster, 1986b). The list of species found in the 20,000 seedling quadrats within the 50 ha plot changes slightly from year to year, as rare species appear and disappear from the census (Comita and Hubbell, unpublished data). Thus, it is not surprising to find small differences in species composition between two samples. Slight differences in species abundances and rank in the seedling layer are also expected due to clumped tree species distributions and annual variation in seed production among individuals, both of which result in patchy seedling distributions (Hubbell and Foster, 1983; De Steven, 1994; Harms et al., 2001). Despite slight differences in species composition, we found no significant differences in the relative abundances of growth forms or of the most common species inside and outside the 50 ha plot.

Our conclusion of no significant trampling effects is based upon data on established seedlings $\geq$20 cm tall. Researcher activity could be impacting smaller seedlings. However, if such impacts are occurring, they do not have any net effect on the seedling community by the time seedlings reach the $\geq$20 cm height class. High natural levels of compensatory mortality during the seed to seedling transition may mask possible effects of researcher impact in this size class (Harms et al., 2000). Our results also suggest that levels of disturbance caused by researcher presence in the plot may be negligible relative to naturally occurring disturbances, such as mammal movements or tree and litter fall. Condit (1995) noted the impact of field crews on the seedling layer, but predicted that their negative effect was small relative to trampling by other mammals moving through the plot on a regular basis. BCI has populations of small mammals, including peccary (*Tayassu tajacu*), which regularly move in groups throughout the island. Naturally occurring physical impacts to seedlings and saplings also include damage and mortality caused by tree and litter fall (Aide, 1987; Clark and Clark, 1991). In comparison to the effects of mammal movement and canopy debris, the impact of research in the plot may be trivial.

In addition, the low-level human disturbance occurring in the 50 ha plot is likely matched by simultaneous processes of recovery (Chazdon, 2003). While the plot is consistently subject to research, the primary tree census represents the most concentrated use and occurs only at 5 year intervals. Tropical forests have demonstrated the ability to recover from much larger one-time disturbances in short periods of time (Guariguata and Ostertag, 2001). Although the annual seedling census is the largest recent research effort, not even localized effects on seedling density were detectable between seedling quadrats and surrounding areas.

It is conversely possible that research activity could have an indirect, positive effect on seedling density in the study area, as researcher presence and trail systems can alter the movements of animals through the forest. Additionally, the disturbance of litter and seed banks by researchers may facilitate an increase in the germination of seedlings (Sheil, 1995). While we did find higher mean seedling density inside of the BCI 50 ha plot compared to adjacent areas, the difference was not statistically significant. Thus, any indirect, positive effects of research activity are minor or may be canceled out by direct negative effects of trampling.

Research may result in plant community changes inside the BCI 50 ha plot that do not fall within the scope of this study or which may exhibit considerable ecological lag prior to detection (Magnuson, 1990). Other factors, such as soil or herbaceous plant communities, may also be impacted by researcher presence and should be studied with sufficient frequency so as to detect subtle long-term changes. Moreover, effects of long-term research are likely to be highly site specific. Steeper topography or higher rainfall may lead to more difficult research conditions and result in greater levels of human disturbance. In recent years, there has been a rise in the number of long-term research sites in forests worldwide thanks to the Long-Term Ecological Research (LTER) program and the Center for Tropical Forest Science's global network of forest dynamics plots. Research to monitor the effects of long-term investigations should be emphasized across these long-term ecological research sites as appropriate.

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