NOTE AND COMMENT

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Intensive research activity alters short-term seedling dynamics in a tropical forest

Abstract Researchers can have unintentional, yet significant effects on their study systems. We tested for the effects of an intensive tree census on seedling dynamics in a 50-ha permanent forest plot on Barro Colorado Island, Panama. At the community level, and for different shade-tolerance guilds, we found no significant differences in seedling recruitment or survival inside compared to controls outside the plot. However, among growth forms, canopy trees and lianas exhibited significantly lower seedling survival inside the plot. Results suggest that intense researcher activity impacts short-term vegetation dynamics, but effects do not accumulate over time.

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Introduction

Researcher presence and activities associated with data collection in the field can have significant direct and indirect effects on the organisms and communities under study (Cahill et al. 2001; Sheil 1995). In forests, understory plants and seedlings are particularly vulnerable to injury due to trampling or breakage by researchers moving through the study area (Goldsmith et al. 2006). Trampling may increase mortality and reduce recruitment of seedlings and small saplings, biasing estimates of population dynamic rates. In addition, because species differ in their ability to tolerate and recover from physical damage (Boucher et al. 1991; Ickes et al. 2003; Yorks et al. 1997), trampling by researchers could potentially cause shifts in the structure and composition of vegetation.

Both in the tropics and elsewhere, intensively sampled forests have become an increasingly important and frequently used tool in long-term studies of vegetation dynamics (Losos and Leigh 2004; Rees et al. 2001). At long-term research sites it is typically assumed that research activities do not influence the organisms or processes under study, yet this assumption has rarely been tested (Wolski et al. 2004). Despite this lack of attention, there is reason to believe that researcher impacts may be significant. In forest plots, periodic censuses typically require large numbers of field workers concentrated in a relatively small area. Such census events may serve as periodic "pulse" disturbances (sensu Bender et al. 1984), with the potential to alter species dynamics over the short-term (Glasby and Underwood 1996; Underwood 1991). Effects of repeated censuses may accumulate over time, resulting in permanent shifts in community composition. Alternatively, vegetation may recover from research-related disturbance between events, leaving little or no

detectable impact on vegetation over the long-term. Nevertheless, short-term responses to discrete research events are of concern since they can bias data collected during or shortly after such events.

Here we test for altered seedling dynamics immediately following a ''pulse'' disturbance originating from a complete census of trees and shrubs in a 50-ha forest dynamics plot on Barro Colorado Island, Panama (BCI). Established in 1980, the BCI 50-ha plot is one of the most rigorously studied areas of tropical forest in the world (Goldsmith et al. 2006). As a result, there has been growing concern about the potential impact of research activities on vegetation in the plot (L. Comita, pers. obs.).

Every 5 years, all freestanding woody stems ≥1 cm DBH in the BCI 50-ha plot are measured, mapped, and identified to species. This tree census is the most intensive study carried out in the BCI plot, requiring 14–16 field assistants working for approximately 9 months (Condit 1998). The large number of researchers walking through the plot during this period may result in the unintentional trampling and killing of understory vegetation. To test for such researcher impacts, we compared seedling dynamics in quadrats located inside and outside the BCI plot during the 2 year interval spanning the 2005 census of trees and shrubs. We expected the higher foot traffic inside the plot during the census to result in higher seedling mortality and lower seedling recruitment in the plot compared to outside the plot. In addition, we hypothesized that trampling may cause shifts in the relative abundances of life history guilds inside the 50-ha plot.

Methods

Study site

Barro Colorado Island (9°9′N, 79°51′W) is a 1,500-ha former hilltop in Central Panama that became isolated from the mainland when the Chagres River was dammed to form a portion of the Panama Canal in 1914. BCI supports old growth and secondary moist tropical forest with an annual rainfall of 2,600 mm and a mean annual temperature of 27°C (Dietrich et al. 1982). Flora, fauna, and abiotic characteristics of the island are described in detail by Leigh (1999) and Leigh et al. (1982). Established in 1980, the BCI 50-ha permanent forest dynamics plot is located 120–155 m a.s.l. on the island's central plateau, and consists primarily of old growth forest with the exception of 2 ha of secondary forest in the northeastern corner of the plot (Hubbell and Foster 1983). The main function of the BCI 50-ha plot is to provide long-term, spatially explicit data on vegetation dynamics used to test hypotheses about the maintenance of diversity in tropical forests (Hubbell and Foster 1983). Research in the plot is therefore limited primarily to non-destructive sampling and measurements, and there are restrictions against collections and manipulations (Goldsmith et al. 2006).

Data collection

In 2001, we began an annual census of seedlings and small saplings in the BCI 50-ha plot. A permanently marked 1-m² seedling quadrat was established in the center of each 5×5 m subquadrat of the 50-ha plot, for a total of 20,000 plots (Comita et al. 2007). Within each quadrat, all free-standing woody plants ≥20 cm tall and <1 cm DBH have been tagged, mapped, and identified to species. Five hundred thirty-nine of the 20,000 quadrats located inside the 50-ha plot are not censused to avoid damaging nearby ongoing research projects. The remaining 19,461 seedling quadrats have been censused annually since 2001, with the exception of 2005 when no seedling census was conducted due to the main tree census that year.

To test for researcher impacts on the seedling layer resulting from the 2005 tree census, we established 600 control quadrats at 5-m intervals around the outside of the 50-ha plot at a perpendicular distance of 20 m from the edge of the plot (Goldsmith et al. 2006). All freestanding woody plants ≥20 cm tall and <1 cm DBH in the control quadrats were initially tagged and mapped in June–July 2004, using methods identical to those used in the census of seedlings inside the 50-ha plot (Comita et al. 2007). We subsequently identified seedlings to species in October–November 2004. Between sampling and identification, 63 seedlings died and an additional 71 seedlings could not be identified. We revisited the quadrats in July 2006, and recorded the status of tagged seedlings (alive/dead) and number of new recruits (≥20 cm tall). A total of 1,544 seedlings were tagged in 2004, and 943 new recruits were counted in 2006.

Although limited research is conducted in the forest adjacent to the 50-ha plot, most research activity is concentrated inside the plot (Goldsmith et al. 2006). Data from control quadrats that were within 2 m of a trail or were noticeably impacted by nearby research were discarded (14 quadrats), leaving 586 quadrats for use in statistical comparisons. Seedling quadrats inside the 50-ha plot and control quadrats outside the plot were both censused in 2004 and 2006, and experienced similar levels of visitation during those censuses. We did not revisit the area adjacent to the 50-ha plot (where the control quadrats were located) between these two censuses, while quadrats inside of the plot experienced elevated levels of researcher activity as a result of the 2005 census of all stems ≥1 cm DBH in the plot. The quadrats outside of the 50-ha plot therefore served as an adequate control for testing potential effects of intense, concentrated researcher foot traffic and other activity associated with a complete census of trees in the BCI plot.

Data analysis

To test for researcher impacts on seedling dynamics, we compared data from the 2004 and 2006 seedling plot censuses conducted inside the 50 ha plot with data taken

over the same interval from the control seedling quadrats adjacent to the 50 ha plot. To test for differences in seedling recruitment inside and outside the BCI plot, we used resampling techniques to generate 95% confidence intervals around the number of recruits per quadrat inside the plot. To account for differences in sample size and to be consistent with the sampling scheme used outside the 50-ha plot, we determined the sampling distribution of the mean inside the plot by randomly drawing 2 x-coordinates and 2 y-coordinates, selecting 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). We selected 596 unique quadrats in total, since the x and y lines cross in four places. This procedure was repeated 1,000 times with replacement, and 95% confidence intervals were generated from the 25th and 975th ranked values of recruit density. The same method was used to determine whether the proportion of seedlings surviving was significantly higher inside versus outside the plot.

To determine the minimal differences that we could detect with our analyses, we calculated the ratio of survival (and recruitment) inside the plot to outside the plot in 1,000 bootstrapped samples. For each of the bootstrap replicates, we resampled with replacement quadrats not only from inside the plot (as described above), but also from outside the plot in order to take into account the variation in both samples. The 25th and 975th ranked values of the ratio of survival (or recruitment) inside to survival (or recruitment) outside the plot correspond to the values for which a significant difference could be detected at the $\alpha = 0.05$ level.

Because species' ability to tolerate and recover from physical damage can vary with life history strategy, we also compared seedling survival inside and outside the plot separately for shade tolerance guilds and growth form guilds. Species were assigned to one of five growth forms 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 (Comita et al. 2007; Hubbell and Foster

1986). Species were also designated as shade-tolerant, intermediate, or light demanding, based on the classification used in Comita et al. (2007) for tree and shrub species. Common shade-tolerant species included the understory species *Faramea occidentalis* (Rubiaceae), the midstory species *Eugenia oerstediana* (Myrtaceae), and canopy species *Tetragastris panamensis* (Burseraceae), *Ocotea whitei* (Lauraceae) and *Trichilia tuberculata* (Meliaceae). Common light demanding species included the understory tree *Croton billbergianus* (Euphorbiaceae), the midstory species *Gustavia superba* (Lecythidaceae) and the canopy species *Chrysophyllum cainito* (Sapotaceae).

Differences between mortality rates inside and outside of the plot were assessed separately for each guild using the method described above. Since new seedlings encountered in quadrats outside the plot in 2006 were not identified to species, analyses of recruitment by guild were not possible. We performed all statistical analyses using the R Statistical Package 2.4.1 (R Development Core Team 2006).

Results

Community-wide seedling survival and recruitment were not significantly different inside the plot compared to adjacent control areas during the 2-year interval spanning the 2005 census. The mean density of recruits outside the plot (1.55 seedlings/m^2) was within the 95% confidence intervals generated around the density of recruits inside the plot (Fig. 1a). Similarly, the overall proportion of seedlings surviving outside the plot (0.775) was within the 95% confidence intervals around the proportion of seedlings surviving inside the 50-ha plot (Fig. 1b). For survival, in 95% of the bootstrapped samples, the ratio of the proportion of individuals surviving inside the plot to the proportion surviving outside the plot fell between 0.97 and 1.08. This indicates that we can exclude (with 95% certainty) the possibility that researcher impacts caused $> 3\%$ decrease in survival inside the plot. For recruitment, in 95% of the bootstrapped

Fig. 1 Histograms of **a** mean number of recruits m^{-2} (≥ 20 cm tall) and **b** proportion of seedlings surviving between 2004 and 2006 in each of 1,000 random draws of 596 seedling quadrats located inside the 50-ha permanent plot on Barro Colorado Island, Panama. *Dashed lines* represent 95% confidence intervals. *Arrows* represent the **a** mean number of recruits m^{-2} and **b** proportion of seedlings surviving for 586 seedling quadrats located outside of the 50-ha plot
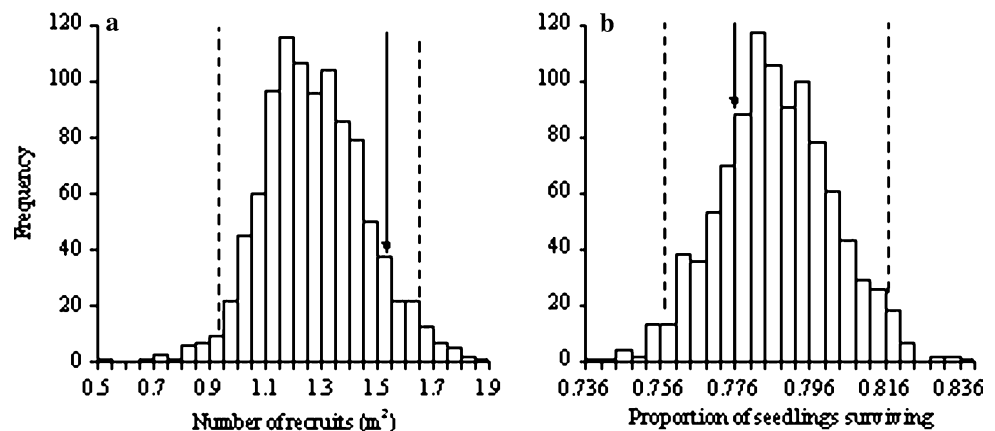
samples, the ratio of the density of new recruits inside to the density of new recruits outside fell between 0.62 and 1.09, excluding the possibility that researcher impacts resulted in a > 38% decrease in recruitment.

In analyses of the effect of research activity on different life history guilds, we similarly found no significant differences in survival inside versus outside the plot when examining shade tolerance guilds separately. The proportion of seedlings surviving outside the plot for individuals classified as shade-tolerant (0.826), intermediate (0.746) and light-demanding (0.773) fell within the 95% confidence intervals around the proportion of seedlings surviving inside the plot (shade-tolerant: 0.800–0.838; intermediate: 0.637–0.784; light-demanding: 0.657–0.800).

In contrast, we found some significant differences in survival inside versus outside the plot when examining each growth form separately. Survival of lianas and canopy trees was significantly higher outside versus inside the 50-ha plot (based on 95% confidence intervals generated by resampling quadrats from within the 50-ha plot), suggesting that these growth forms were negatively impacted by researcher trampling (Table 1). In contrast, shrubs, understory and midstory trees did not exhibit significant differences in seedling survival (Table 1).

Discussion

We found significant impacts on seedling dynamics inside the BCI 50-ha plot immediately following the intense research activity associated with a complete census of trees and shrubs ≥1 cm DBH. Specifically, there were significant differences in survival inside versus outside the plot for canopy tree and liana seedlings, although not for other growth forms. Tropical tree seedlings and saplings often experience naturally occurring physical impacts from ground-dwelling animals moving through the forest and from falling branches and litter from the canopy (Aide 1987; Clark and Clark 1991; Paciorek et al. 2000). In the BCI forest, damage to

woody plants is frequent and many species are able to respond by resprouting (Paciorek et al. 2000). Species that spend their lives in the understory likely experience more stem damage than species that reach the canopy, and thus may be better adapted to tolerate and recover from physical damage (Ickes et al. 2003). This may explain why canopy trees and lianas, the only two guilds that reach the canopy, exhibited significantly lower survival inside compared to outside the plot.

In contrast, at the community level and for the majority of life history guilds examined, we found little evidence of researcher impacts on seedlings, suggesting that most understory vegetation in the BCI 50-ha plot is not negatively affected by human trampling. During the census of trees and shrubs in the plot, field workers typically work alone or in pairs, censusing plants in a 20-m-wide column of the plot, moving from south to north. Each column is subsequently visited a second time by one of the supervising botanists to check species identifications and measurements. Therefore, even though a large field crew is needed to sample the entire plot, the impact is reduced by minimizing the number of people visiting any given area. In contrast, trampling effects are more evident along trails, which experience high foot traffic during the censuses (Comita and Goldsmith 2008).

We originally hypothesized that the periodic censuses of trees in the BCI plot act as "pulse disturbances", causing lowered rates of seedling survival and recruitment as a result of trampling by researchers. The results presented here suggest that trampling impacts during intense pulses of research activity can cause short-term changes in seedlings dynamics for some growth forms. Such alterations to seedling dynamics could accumulate over time and cause shifts in the seedling layer. Given the lower survival of canopy trees and lianas inside the plot during our study, we would expect a decline in the relative abundance of these guilds. However, the proportion of stems assigned to these two growth forms inside the plot was slightly higher in 2006 than in 2004 (Table 1). This suggests that, although significant, the trampling effect was not strong enough to alter the relative abundance of

Table 1 Seedling survival outside versus inside the Barro Colorado Island 50-ha permanent plot between 2004 and 2006 for five different growth forms

Growth form	Survival outside (%)	Survival inside (%)	Inside 95% CIs	Proportion of stems inside	
				2004	2006
Shrubs	84.4	86.4	83.0–90.3	0.209	0.197
Understory trees	81.0	82.6	77.6–86.9	0.161	0.153
Midstory trees	87.8	82.9	76.8–88.6	0.121	0.121
Canopy trees	**78.7**	71.9	65.6–78.1	0.301	0.308
Lianas	**86.3**	80.0	74.6–84.5	0.187	0.195

Percent survival outside the plot was considered significantly different from inside the plot (in bold) if values fell outside of the 95% confidence intervals generated by resampling quadrats from within the 50-ha plot. Despite significantly higher survival of canopy tree and liana seedlings outside compared to inside the 50-ha plot, the proportion of stems inside the plot assigned to those growth forms increased slightly between 2004 and 2006

growth forms inside the plot over the course of our study or that it was offset by high recruitment of liana and canopy tree species during the study period. Furthermore, in a previous analysis, we found no difference in seedling density, size class distribution, or the relative abundances of growth forms in the seedling layer inside compared to outside the BCI plot (Goldsmith et al. 2006). Thus, there is little evidence of permanent shifts in the seedling layer due to researcher activity in the BCI 50-ha plot. Nonetheless, significant short-term impacts may bias results of studies conducted during or shortly after intensive bouts of research activity and should therefore be considered when drawing conclusions from data collected during affected periods. Additional studies are needed to quantify the length of time needed for vegetation to recover from such impacts.

The handful of previously published studies that have explicitly tested for effects of research-related activities on plant communities have also failed to detect strong researcher impacts (Castilho et al. 2006; Phillips et al. 1998; van Mantgem and Stephenson 2004; Wolski et al. 2004). In forest systems, these studies have focused on impacts of collecting techniques on saplings and trees. Phillips et al. (1998) found no significant reduction in survival of tropical trees that had small branches collected for identification as compared to uncollected individuals over a 5 year period. Castilho et al. (2006) found no difference in plant performance between trees climbed with spikes and unclimbed trees in a Brazilian forest over an interval of 14–28 months. Similarly, van Mantgem and Stephenson (2004) found no effect of increment coring on tree mortality for two coniferous species in the Sierra Nevada of California, USA.

The BCI plot is part of a global network of forest dynamics plots coordinated by the Center for Tropical Forest Science (CTFS). These large (2–52 ha) forest plots use identical methodology to study the biology and dynamics of both temperate and tropical forests, and to make comparisons among sites (Losos and Leigh 2004). Although our results suggest that the censuses of these plots may impact short-term vegetation dynamics, these effects appear to be limited to certain growth forms and do not accumulate over time. Nonetheless, effects of researcher presence will ultimately vary from site to site, depending on factors such as data collection techniques and frequency, trail systems, climate, and topography. Therefore, we encourage tests of researcher impacts on vegetation dynamics at additional study sites. Quantifying these impacts will ultimately result in more robust conclusions from large-scale, long-term studies of vegetation dynamics.

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