

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

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Received 21 March 2006; received in revised form 9 June 2006; accepted 10 June 2006

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 m² 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. © 2006 Elsevier B.V. All rights reserved.

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 ≥ 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 $5 \text{ m} \times 5 \text{ m}$ 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 ($9^{\circ}9'N$, $79^{\circ}51'W$), 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 ≥ 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).

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