

Impact of Research Trails on Seedling Dynamics in a Tropical Forest

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ABSTRACT

We evaluated the impact of research access trails on adjacent seedling density, survival, and recruitment in a permanent tropical forest plot in Panama. Significant differences were detected up to 20 m from trails, indicating that data collected close to trails may be biased. However, observed effects were not substantial enough to affect plot-wide estimates of seedling dynamics, suggesting that research trail impacts are negligible when affected areas constitute only a small fraction of the total area sampled.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: Barro Colorado Island; forest dynamics plot; long-term ecological research; Panama; research impact; seedling community; trampling.

IN THE PAST TWO DECADES, there has been a substantial increase in the number of permanent, long-term study plots in tropical forests (Condit 1995, Rees *et al.* 2001, Malhi *et al.* 2002, Losos & Leigh 2004). This has led to increasing concern regarding impacts associated with researcher activities at these intensively studied sites (Sheil 1995, Malhi *et al.* 2002, Phillips *et al.* 2002). Even in nonmanipulative studies, unintentional physical impacts to vegetation by researchers during data collection may artificially alter the dynamics and processes under investigation (Goldsmith *et al.* 2006).

The most obvious and direct effect of research activity is the trampling of understory plants as researchers move through the study site. Trampling is likely to be most concentrated along frequently used trails within study areas. Previous studies have documented changes to seedling recruitment, mortality, and soil properties along trails; however, these studies have focused predominantly on recreational trails in temperate regions (*e.g.*, Kuss 1986, Boucher *et al.* 1991, Sun & Liddle 1993). Trails open exclusively to researchers can experience similar rates of use and may therefore also suffer from changes to vegetation and soils. If these changes are substantial or extend beyond trail edges, they could bias estimates of vegetation dynamics and forest structure.

In this study, we sought to quantify the significance and spatial extent of research trail impacts on the structure and dynamics of the seedling layer in the 50-ha permanent forest dynamics plot on Barro Colorado Island (BCI), Panama (Hubbell & Foster 1983). Established in 1980, the BCI plot is one of the most intensively studied

areas of tropical forest in the world (Goldsmith *et al.* 2006). Long-term research in the plot includes extensive tree, seed, seedling, and canopy censuses, as well as long-running studies of animal populations. An established and well-maintained network of trails runs throughout the plot and experiences daily traffic by researchers working in or walking through the plot to access other areas of the island. BCI hosts approximately 250 scientists annually. On average, there are 25 researchers staying on BCI and 15–20 additional researchers who commute to the island each day. Approximately half of these researchers regularly use the trails running through the plot to access other areas of the island (O. Acevedo, pers. comm.). The number of people working within the 50-ha plot on any given work day ranges from six to 12, with up to 20 people present in the plot during the main census of trees, which occurs every 5 yr. Given the frequent use of the trail system, we expected lower seedling recruitment and survival directly on trails due to trampling. However, since changes to canopy structure associated with trail establishment lead to increased understory light availability, we also predicted an increase in seedling recruitment and survival in areas adjacent to trails.

BCI (9°9' N, 79°51' W) is a 1500 ha former hilltop that became isolated from the mainland when the Chagres River was dammed to form Gatún Lake in 1914 (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.* 1982). The BCI 50-ha permanent forest dynamics plot is located on the island's central plateau 128–155 m asl and consists primarily of old-growth forest with the exception of 2 ha of secondary forest in the northeastern corner of the plot (Hubbell & Foster 1983). There are *ca* 3 km of trails running through the BCI plot, ranging from 0.5 to 1 m wide (average trail width = 62 cm). Cinder blocks have been placed every *ca* 0.5 m along a short stretch of trail running through a swampy area of the plot.

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TABLE 1. Seedling community structure and dynamics as a function of distance from trail in the BCI 50-ha plot, Panama. Mean density, proportion surviving and number of new recruits were calculated for seedling quadrats grouped into 5-m distance classes, and separately for quadrats falling directly on trails (< 0.5 m). Values considered significantly different from random (in bold) fell outside of 99% CIs generated from 1000 random draws from the pool of all seedling quadrats in the plot.

Distance from trail (m)	No. of quadrats	Seedling density (per m ²)			Recruitment (per m ²)		Survival	
		2001	2002	2003	2001–2002	2002–2003	2001–2002	2002–2003
< 0.5	112	1.98	2.05	2.05	0.259	0.348	0.942	0.856
0.5–4.9	683	4.16	4.12	3.98	0.388	0.476	0.916	0.884
5–9.9	645	3.08	3.03	2.97	0.267	0.372	0.901	0.873
10–14.9	705	2.95	2.90	2.85	0.240	0.372	0.907	0.879
15–19.9	740	2.94	2.90	2.81	0.269	0.351	0.914	0.868
20–24.9	752	2.94	2.93	2.94	0.282	0.441	0.900	0.880
25–29.9	709	3.01	3.05	3.08	0.299	0.444	0.928	0.869
30–34.9	673	3.03	3.12	3.10	0.314	0.421	0.924	0.874
35–39.9	684	3.39	3.36	3.50	0.308	0.572	0.916	0.881
40–44.9	628	3.28	3.41	3.44	0.412	0.439	0.919	0.887
45–49.9	622	3.33	3.36	3.36	0.312	0.506	0.913	0.876
All distances	13881	3.17	3.21	3.23	0.361	0.480	0.914	0.876

In 2001, we established one permanently marked 1-m² seedling quadrat in the center of each 5 × 5 m subquadrat of the 50-ha plot, for a total of 20,000 quadrats (Comita *et al.* 2007). Within each quadrat, all freestanding woody plants ≥ 20 cm tall and < 1 cm dbh were tagged and mapped on an annual basis between 2001 and 2003 (with the exception of 640 quadrats that were not censused to avoid damaging nearby preexisting research plots). Here, we use data from the seedling censuses to test for impacts of trail use on seedling community structure and dynamics.

We established the exact location of trails by referencing them to previously tagged trees at regular intervals. As all trees ≥ 1 cm dbh within the 50-ha plot are tagged and mapped to the nearest 1 m (Hubbell & Foster 1983, Condit 1998), we were able to use these data to generate a map of all trails and calculate the distance from the center of each seedling quadrat to the center of the nearest trail. Quadrats within 50 m of the trail were grouped into 5-m distance classes (Table 1). In the nearest distance class, we separated out quadrats < 0.5 m from the nearest trail, since those quadrats fell directly on trails. All quadrats within 50 m of the edge of the 50-ha plot were excluded, as we did not know their proximity to trails located outside of the plot.

We used resampling methods to test for effects of trail proximity on seedling density in all years, and on the proportion of seedlings surviving and number of seedlings recruiting into the ≥ 20 cm size class during the 2001–2002 and 2002–2003 intervals. Specifically, we tested whether the quadrats in each distance class were significantly different from a random sample of quadrats drawn from across the entire 50-ha plot. To control for possible differences in habitat between the samples being compared, we used the habitat classification of Harms *et al.* (2001), which assigns each 20 × 20 m

section of the 50-ha plot to one of seven edaphic habitat types. For each distance class, we determined the number of quadrats assigned to each of the seven habitat types and then randomly drew an identical number of quadrats from the pool of all quadrats in the plot assigned to that particular habitat type. Therefore, the random sample contained the same total number of quadrats and the same proportion of quadrats in each habitat type as the distance class being evaluated. We then combined the quadrats from all habitats and calculated the mean density, proportion survival, and number of recruits in the random sample. This procedure was repeated 1000 times and the ranked values were used to generate confidence intervals. Because of the multiple tests employed, we used more conservative 99% CIs to assess statistical significance. The resampling program for generating confidence intervals was written and executed with R Statistical Package 2.1.0 (R Development Core Team 2005).

We detected significant effects of trails on seedling density and recruitment up to 20 m away, but found no significant effects on seedling survival (Table 1). Results were qualitatively similar when excluding the short stretch of trail with cinder blocks (data not shown). Seedling density in all years was significantly lower directly on trails (< 0.5 m). As trails in the BCI plot are well defined and frequently used, these seedlings are subject to the highest intensity of trampling. In contrast, seedling density adjacent to trails (0.5–4.9 m) was significantly higher than the mean density across the 50-ha plot in all years. Recruitment showed a similar, although nonsignificant trend, with the mean density of recruits lower directly on trails and higher immediately adjacent to trails (Table 1). In closed-canopy tropical forests such as BCI, understory plants are typically light-limited (Harms *et al.* 2004). Thus, even

small increases in available understory light associated with trails likely enhance recruitment and support higher seedling densities.

In contrast to the increases in seedling density and recruitment in the 0.5–4.9 m distance class, we detected significant decreases in the number of recruits per quadrat at 5–14.9 m in 2002 and at 15–19.9 m in 2003 (Table 1). Similarly, in 2003 we detected significantly lower seedling density in the 15–19.9 m distance class. Together, these results suggest that negative effects on recruitment, presumably due to trampling, extend up to 20 m away from trails, but are masked at closer distances by the positive effects of increased understory light levels immediately adjacent to trails. Trampling effects up to 20 m from trails may be due to the fact that researchers locate frequently sampled quadrats or focal individuals close to trails for convenience. For example, in the BCI plot, seed traps located 4–10 m away from trails have been checked weekly since 1987 (Wright *et al.* 2004). Similarly designed seed trap networks have also been established in tropical forest plots in South America and Asia (L. Comita, pers. obs.). As a result of such sampling schemes, areas near trails experience increased foot traffic. However, overall impact on the plot is reduced since researcher movement during data collection is largely confined to the main trail system and areas immediately adjacent to trails.

The observed effects of trails on seedling density and recruitment may result not only from researcher activity, but also from shifts in animal movement patterns due to the presence of trails. Shifts in animal movements can potentially alter patterns of seedling trampling, seed predation, seed dispersal, and vertebrate herbivory. The contribution of an individual animal species to seedling dynamics depends on its associated life-history characteristics. Although trails may facilitate easy movement for species such as larger predatory mammals, smaller animals like paca (*Agouti paca*) generally travel more off trail (Weckel *et al.* 2006). Many tropical vertebrates are also less likely to travel on trails with sustained human presence, thereby increasing rates of nocturnal, arboreal, or off-trail movement (Griffiths & Van Schaik 1993). Alternatively, some species may experience degrees of habituation to human presence on trails. Certain bird species are less likely to flush when encountering humans traveling down established trails in comparison with indirect off trail approaches (Fernández-Juricic *et al.* 2004). Long-term research conducted with camera traps on BCI has revealed both preferential mammal movement on trails and seasonal patterns of movement based on fruiting trees (J. Willis, pers. comm.). Thus, the presence of trails and researchers in the BCI plot may well alter movement patterns of animal species and contribute to the shifts in seedling density and recruitment on and near trails. Additional studies on individual animal species' behavior are needed to gain an accurate depiction of how trail-mediated shifts in animal movements contribute to changes in seedling dynamics.

The lack of significant effects of proximity to trail on seedling survival suggests that larger, established seedlings, such as those included in our study (*i.e.*, ≥ 20 cm tall), are less vulnerable to trampling than seeds or newly germinated seedlings. Differences in susceptibility to trampling may vary not only with size, but also

among species. Harms and Dalling (1997) found that larger seeded tropical tree and liana species are better able to resprout after damage. Such species are able to tolerate higher levels of trampling, and may therefore increase in abundance relative to more susceptible species on or near trails. In addition, increased light levels adjacent to trails may favor seedlings of light-demanding species. Thus, the observed community-level differences in seedling density and recruitment on and near trails may also be accompanied by shifts in species composition.

Having detected significant effects of trails on vegetation structure and dynamics, we further tested whether the observed effects were strong enough to bias estimates of seedling density, survival, and recruitment in the BCI plot. We compared estimates made using all seedling quadrats within the 50-ha plot to estimates made excluding seedling quadrats close to trails using Kolmogorov–Smirnov tests. As there were multiple ties in the data sets, we used a bootstrap version of the univariate Kolmogorov–Smirnov test (available in the 'Matching' package for R), which uses Monte Carlo simulations to determine the proper P -value. Estimates of seedling density, survival, and recruitment did not change when excluding seedling quadrats ≤ 5 m or ≤ 20 m away from trails ($P \gg 0.05$, for all comparisons in all years). Thus, despite being locally significant, the influence of trails on nearby vegetation is not substantial enough to affect plot-wide estimates of seedling dynamics. Trails in the BCI 50-ha plot cover an area of *ca* 2000 m², which represents just 0.4 percent of the total area. If trail impacts extend 20 m, approximately 12 percent of the plot would be affected; however, these effects do not appear to be sufficiently strong to bias estimates of vegetation dynamics.

Overall, our results indicate that calculations of vegetation structure and dynamics at the scale of the entire BCI 50-ha plot are not altered by the impacts of research trails. In a previous study, we have also shown that seedling community structure and composition in the BCI plot do not differ from areas experiencing less research activity outside of the plot (Goldsmith *et al.* 2006). Taken together, these results suggest that long-term, intensive research in the BCI plot has not biased estimates of vegetation structure and dynamics. At other sites, the proportion of total plot area falling within the zone of trail impact will determine whether research trails have significant effects on plot-wide estimates of vegetation structure and dynamics.

Although BCI currently hosts more scientists than most other tropical research stations, the volume of traffic experienced in the BCI plot is expected to become more common at other sites as the increasing emphasis on long-term, plot-based research in the tropics continues. The strength of trail effects will likely vary among sites depending on the vulnerability of vegetation to trampling, rates of trail use, and trail maintenance regimes. In particular, trail conditions may deteriorate more rapidly at sites with higher rainfall or steeper topography, resulting in intensified impacts on surrounding vegetation. In long-term forest plots with multiple ongoing projects, researchers and plot managers should work together to minimize impacts and ensure that all data collected are representative. We further recommend that all scientists carefully consider potential

research impacts when designing sampling schemes and trail systems at tropical research sites.

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