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SHORT COMMUNICATION

Seed bank dynamics in five Panamanian forests

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Many tropical pioneer species depend on the presence of high seed densities in the soil for successful recruitment following canopy disturbance (Cheke *et al.* 1979, Dalling & Hubbell 2002, Guevara Sada & Gómez Pompa 1972, Whitmore 1983). However determinants of variation in the composition and abundance of soil seed banks remain poorly understood. Seed bank densities can be affected by rates of seed predation and pathogen infection on the surface and in the soil, by intrinsic rates of loss in viability following dispersal, and by variation in the timing and duration of fruit production (Dalling *et al.* 1997, Garwood 1983, Murray & Garcia 2002). Here we compare seasonal fluctuations in seed bank density in five Panamanian forests varying in elevation and seasonality of precipitation (Table 1). We predict that lowland forests should show stronger intra-annual fluctuation in seed bank densities than montane forests because seed production and loss rates should be higher under conditions of greater resource availability, and where consistent high temperatures support greater abundance or activity of seed predators and pathogens (Brühl *et al.* 1999). Secondly, among lowland sites, we predict greater fluctuations in seed bank densities at drier, more seasonal sites where seasonally favourable conditions for seedling recruitment may select for interspecific synchrony in fruit production (Daubenmire 1972, Garwood 1983).

To test these predictions we concurrently sampled the soil seed bank at the five sites. Three of these sites, Parque Metropolitano, Barro Colorado Island (BCI) and Fort Sherman span the lowlands of the Isthmus of Panama and a gradient in rainfall and seasonality. One additional site, Cerro Campana, is also in the Panama Canal watershed in central Panama, at higher elevation and lacking seasonality. These four sites are floristically well-described with representative permanent tree plots (Pyke *et al.* 2001). The final site, Fortuna, is at high elevation in western Panama and lacks detailed information on floristic composition. With the exception of Parque Metropolitano, all sites are within old-growth forest, with canopies dominated by shade-tolerant species absent from the seed bank. Accessible old-growth forest, however, no longer occurs on the seasonal Pacific coast of Panama, and therefore we used the 60-y-old secondary forest at Parque Metropolitano where the pioneer species *Luehea seemanii*, *Cecropia peltata* and *Trema micrantha* are common in the canopy. The first set of samples were collected in January 2001, corresponding to the end of the wet season in lowland Panama when the soil seed bank density is lowest on BCI (Dalling *et al.* 1997), and 6 mo later in June 2001 during the early wet season when BCI seed bank densities are highest. At each site we collected 60 soil samples 5 m apart along transects (see also Fornara & Dalling, in press). Sample locations were flagged in January, and a second sample, 30 cm from the first, was removed in June. Soil was collected using a 10.3-cm-diameter, 3-cm-deep soil corer to yield a 250-cm^2 sample.

Samples were collected from 0–3 cm depth since seed abundance and diversity is highest in this layer and represents the greatest soil depth from which many seed-bank species can successfully emerge (Pearson *et al.* 2002). Samples were transported in black polythene bags and processed within 36 h of collection. Soil samples were transferred to a growing house at the Smithsonian Tropical Research Institute in Panama City, and placed in 0.125-m^2 trays containing a 2-cm-deep layer of moist seed-free sand. Soil samples were spread evenly to a depth of 0.5 cm, and seedling emergence was recorded over an

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Table 1. Location and characteristics of the five study sites: Parque Metropolitano (PM), Barro Colorado Island (BCI), Fort Sherman (FS), Cerro Campana (CC), Fortuna (F).

Site	PM	BCI	FS	CC	F
Location	8°58′N, 79°34′W	9°10′N, 79°51′W	9°17′N, 79°58′W	8°40′N, 79°52′W	8°43′N, 82°14′W
Elevation (m)	50	70	70	800	1100
Rainfall (mm y^{-1})	1740	2700	3500	2700	3300
Forest type	seasonal semi-deciduous	seasonal semi-deciduous	aseasonal wet forest	pre-montane wet forest	montane wet forest

Table 2. Mean ± SE soil seed bank density (seeds m^{-2}) at each site (n = 60 samples per site) in January and June 2001, for trees and shrubs, and June seed density as a per cent of January value.

	Metropolitano	Barro Colorado	Fort Sherman	Cerro Campana	Fortuna
January	778 ± 72	224 ± 25	138 ±15	380 ± 28	328 ± 36
June	1006 ± 73	792 ± 46	364 ± 37	564 ± 49	270 ± 25
(%)	129	354	263	148	82

8-wk period (see Dalling *et al.* 1995 for an evaluation of this method). Germination trays were arranged randomly in the growing house, and kept moist using an automatic mist watering system. Seedling emergence was recorded at weekly intervals. Specimens of seedlings that could not be identified after 8 wk were individually potted and grown up until taxonomic and life-form identification was possible, however some groups (e.g. Melastomataceae, *Cecropia*, *Piper*) could not be identified beyond the family or genus level.

We recorded in total 47 taxa of trees and shrubs, 14 taxa of climbing plants (lianas and vines) and 14 herbaceous taxa. Comparisons of richness of seed-bank-forming taxa among sites are hampered by differences in our ability to differentiate species at these sites. Nonetheless, we found rather similar total taxon diversity at Parque Metropolitano (22–26 taxa, January–June), BCI (20–23), and Cerro Campana (21–26), somewhat lower diversity at Fort Sherman (15–16) and the lowest diversity at our least well-described site (in terms of species composition) at Fortuna (13–14). The majority of taxa at all sites were trees and shrubs.

Among-site analyses of seed densities presented here are restricted to germinants of woody species (trees and shrubs). Seedling emergence counts from each soil sample were log(count+1)-transformed and analysed by repeated-measures ANOVA, using the general linear model function in SYSTAT (Wilkinson *et al.* 1992). The standing crop of seeds present in the surface 0–3 cm of soil varied up to three-fold among sites (df = 4, 295, F = 38.8, P < 0.001), sample periods (df = 1, 295, F = 192, P < 0.001), and within a site (BCI) between January and June 2001 (Table 2). Seed density was highest in both January and June at Parque Metropolitano, the most seasonal site and the youngest forest, which is dominated by pioneer species in the canopy (Table 2). Contrasts between the three low-elevation sites (Parque Metropolitano, BCI, Fort Sherman) and the two higher-elevation sites (Cerro Campana and Fortuna) revealed that seed densities were not significantly different between these groups in January 2001 (df = 1, 295, F = 3.1, P = 0.08), but were highly significantly different by June 2001 (df = 1, 295, F = 44.4, P < 0.001, Table 2). This reflected a greater wet-season increase in seed density at the low-elevation sites than at the two higher-elevation sites (df = 1, 295, F = 80.8, P < 0.001; Figure 1). For the highest elevation site, Fortuna, seed densities were not significantly different in January and June (df = 1, 59, F = 0.88, NS). Among the old-growth forests seed densities were rather similar in January, with the lowest density at Fort Sherman.

These results provide support for the first prediction of higher seasonal variation in seed density at low-elevation sites (Table 2). This may reflect either lower seasonal loss of seeds from the soil at high elevation or less synchronous fruiting phenologies at these sites. We suspect that differences in seed loss rates are probably not responsible for this result. In a separate study we found that seed predation rates for pioneer seeds on the soil surface are similar among these sites (Fornara & Dalling 2005). Further, seeds of *Cecropia* showed strong seasonal shifts in density at both Cerro Campana and Fortuna, suggesting that super-annual accumulation of seeds may not commonly occur (see also Murray & Garcia 2002 for data from montane forest in Costa Rica).

Our second prediction that more climatically seasonal lowland sites would show stronger seasonal variation in seed density was not supported. Parque Metropolitano, with the lowest annual rainfall and a 4-mo dry season, showed rather little variation compared with BCI and Fort Sherman. Low variation at Parque Metropolitano is mostly attributable to the high densities of *Muntingia calabura* at this site. This species fruits throughout the year (Croat 1978), and is probably mostly dispersed into the site by birds from deforested areas surrounding the park. Fort Sherman, our least-seasonal lowland site, had lower seasonal turnover in seed density than Barro Colorado Island, but also had rather low seed densities. While this may reflect biotic factors (lower seed inputs and higher seed losses), Sherman soil was also more clay-rich than at other sites. This may be an important factor confounding across site comparisons of soil seed banks. Clay-rich soils are much more difficult to spread evenly in germination

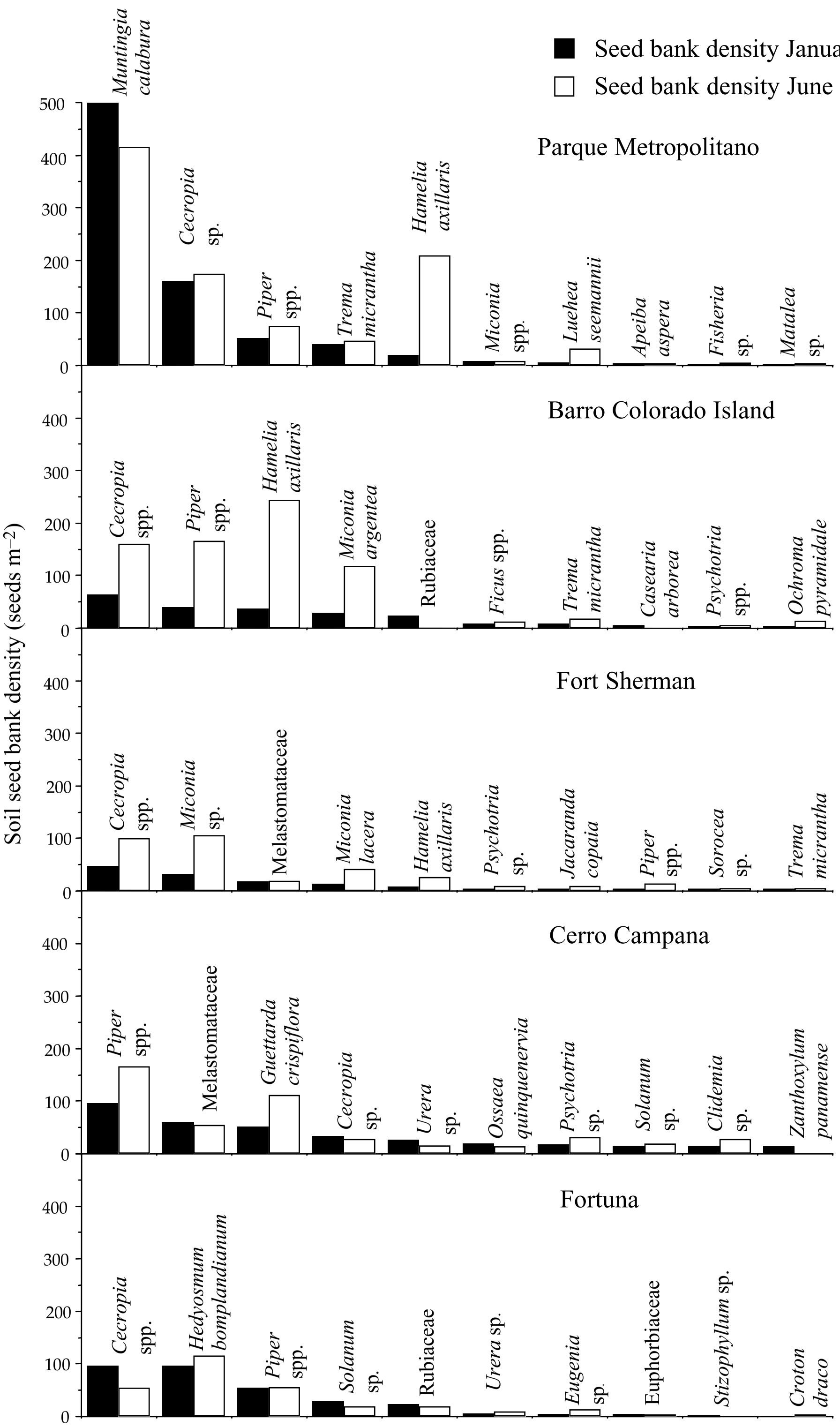

Figure 1. Rank abundance of the ten commonest taxa (seeds m^{-2}) present in the surface 0–3 cm of soil present at each of five sites censused in January and June 2001.

flats. Low estimated viable seed densities from this site may reflect low seedling emergence success of seeds embedded within larger soil aggregates.

Overall, our results suggest soil seed bank dynamics are more dependent on reproductive phenologies in highly seasonal lowland forests in central Panama (i.e. Parque

Metropolitano and BCI) where seed input is strongly cued by the 4-mo dry season than in the aseasonal lowland forest of Fort Sherman, and the two higher-elevation sites where rainfall is more consistent through the year. Indeed, at the seasonal lowland sites most tree species flower and fruit during the dry season and early wet season (Foster & Brokaw 1982, Wright & Calderón 1995) resulting in the highest seed bank densities in May-June (Dalling *et al*. 1997).

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