

Conservation Biology

Volume 23 • No. 5 • October 2009



The Journal of the Society for Conservation Biology

Wiley-Blackwell

ISSN 0888-8892



Canopy Seed Banks as Time Capsules of Biodiversity in Pasture-Remnant Tree Crowns

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Abstract: *Tropical pastures present multiple barriers to tree regeneration and restoration. Relict trees serve as "regeneration foci" because they ameliorate the soil microclimate and serve as safe spots for dispersers. Here, we describe another mechanism by which remnant trees may facilitate pasture regeneration: the presence of seed banks in the canopy soil that accumulates from decomposing epiphytes within the crowns of mature remnant trees in tropical cloud forest pastures. We compared seed banks of canopy soils (histosols derived from fallen leaves, fruits, flower, and twigs of host trees and epiphytes, dead bryophytes, bark, detritus, dead animals, and microorganisms, and dust that accumulate on trunks and the upper surfaces of large branches) in pastures, canopy soils in primary forest trees, and soil on the forest floor in Monteverde, Costa Rica. There were 5211 epiphytic and terrestrial plant seeds in the three habitats. All habitats were dominated by seeds in a relatively small number of plant families, most of which were primarily woody, animal pollinated, and animal dispersed. The density of seeds on the forest floor was greater than seed density in either pasture-canopy or forest-canopy soils; the latter two did not differ. Eight species in 44 families and 61 genera from all of the habitats were tallied. There were 37 species in the pasture-canopy soil, 33 in the forest-canopy soil, and 57 on the forest floor. Eleven species were common to all habitats. The mean species richness in the pasture canopy was significantly higher than the forest canopy ($F = 83.38$; $p < 0.02$). Nonmetric multidimensional scaling ordination revealed that the communities were distinct. Greenhouse experiments verified that many of these seeds were viable, with 29 taxa germinating (23 taxa in pruned mats [mimic of exposed conditions] and 16 taxa in control mats [intact conditions]) within 2 months of observation. Nearly half the species that germinated were characteristic of primary forests (primary forest samples, 19%; pasture samples, 29%). This supports the idea that canopy seed banks of pasture trees can function as time capsules by providing propagules that are removed in both space and time from the primary forest. Their presence may enhance the ability of pastures to regenerate more quickly, reinforcing the importance of trees in agricultural settings.*

Keywords: biodiversity conservation, Monteverde, pasture tree, regeneration foci, relict tree, remnant tree, seed bank, tropical cloud forest

Bancos de Semillas en el Dosel como Cápsulas de Tiempo de Biodiversidad en las Copas de Árboles Remanentes en Potrerros

Resumen: *Los potreros tropicales presentan múltiples barreras a la regeneración y restauración de árboles. Los árboles relictos funcionan como 'focos de regeneración' porque mejoran el microclima del suelo y porque fungen como sitios seguros para dispersores. Aquí, describo otro mecanismo mediante el cual los árboles remanentes pueden facilitar la regeneración en los potreros; la presencia de bancos de semillas en el suelo que se acumula en el dosel por la descomposición de epífitas en las copas de árboles maduros remanentes en potreros en bosques de niebla tropicales. Comparé los bancos de semillas en los suelos de las copas (histosoles derivados de hojas, frutos, flores y ramitas de árboles huésped y epífitas, briofitas muertas, corteza, detritos, animales muertos, microorganismos y polvo que se acumulan en los troncos y en la superficie superior de las ramas) de árboles en potreros, en árboles en bosque primario y suelo en de bosque en Monteverde, Costa Rica. Hubo 5211 semillas de plantas terrestres y epífitas en los tres hábitats. Todos los hábitats fueron dominados*

por semillas de un número relativamente bajo de familias, la mayoría de la cuales son leñosas, polinizadas y dispersadas por animales. La densidad de semillas sobre el suelo del bosque no fue mayor que la densidad de semillas en los suelos de copa de potrero ni de bosque; estos últimos no fueron diferentes. Ocho especies en 44 familias y 61 géneros de todos los hábitats fueron contadas. En el suelo de copa de potrero hubo 37 especies, 33 en el suelo de copa de bosque y 57 en el suelo de bosque. Once especies fueron comunes en todos los hábitats. La riqueza de especies promedio en el suelo de copa de potrero fue significativamente mayor que el de bosque ($F = 83.38$; $p < 0.02$). La ordenación de escalamiento multidimensional no métrica reveló que las comunidades eran diferentes. Experimentos de invernadero revelaron que muchas de estas semillas eran viables, 29 taxa germinaron (23 taxa en esterillas [mímica de condiciones expuestas] y 16 en esterillas control [condiciones intactas] en dos meses de observación. Casi la mitad de las especies que germinaron fueron características de bosques primarios (muestras de bosque primario, 19%, muestras de potrero, 29%). Esto soporta la idea de que los bancos de semillas en las copas de árboles de potrero pueden funcionar como cápsulas de tiempo al proporcionar propágulos que son removidos del bosque primario en espacio y tiempo. Su presencia puede incrementar la habilidad de los potreros para regenerar más rápidamente, lo que refuerza la importancia de los árboles en paisajes agrícolas.

Palabras Clave: árbol en potrero, árbol relicto, árbol remanente, banco de semillas, bosque de niebla tropical, conservación de la biodiversidad, foco de regeneración, Monteverde

Introduction

Enhancing biological diversity and ecosystem services in tropical agricultural landscapes is critical for world conservation (Lamb et al. 2005; Harvey et al. 2008). Fragments of tropical forest almost always decline in species richness after the isolation that follows agricultural clearing, but many plant and animal species can persist in individual relict trees (Harvey et al. 2008). These relict (or remnant) trees that were part of the original forest prior to land clearing provide legacy characteristics and may sustain their ecological functions after the landscape has been altered (Holl et al. 2000). For example, in Monteverde, Costa Rica, over 5500 remnant trees in 190 species have been documented on 24 farms, over half of which were primary forest trees that provide resources for forest animals (Harvey & Haber 1999). Monteverde farmers cited 19 reasons for their retention (e.g., shade for cattle, timber, medicines, fruit, medicines, fenceposts, and providing resources for showy and sought-after birds). In Monteverde, a combination of conservation easements, environmental education, reforestation, and economic incentives for landowners has reconnected habitat for the Resplendent Quetzal (*Pharomachrus mocinno*) and enhanced the region for bird-watching ecotourism, bringing critical capital to this rural region (Powell & Bjork 2003, 2004).

In undisturbed forests trees generally regenerate from vertebrate-dispersed propagules in soil seed banks, which store seeds of shade-intolerant species (Vazquez-Yanes & Orozco-Segovia 1993). Seeds rest in the upper horizons of the forest floor for days to decades until environmental changes signal proper growing conditions (i.e., increased levels of sunlight following the opening of a gap from a major branch or tree fall (Lawton & Putz 1988)). In pastures, however, tree regeneration is

more problematic. Over 200 studies have documented aspects of tropical pasture environments that create regeneration barriers for restoration (e.g., Turner & Corlett 1996; Martinez-Garza & Howe 2003; Sampaio et al. 2007). Abiotic factors such as the hotter, drier microclimate of open pastures limit many species vulnerable to exposed conditions. Soil compaction due to trampling by livestock deters seedling survival. Over the long term, seed banks in pastures typically become dominated by ruderals and early-successional plants (mainly wind-pollinated and wind-dispersed seeds) that compete with established vegetation for sunlight, water, and nutrients (Tekle & Bekele 2000; Zimmerman et al. 2000).

A critical factor limiting forest recovery in tropical pastures is lack of seed availability (Holl 1999; Holl & Kappelle 1999; Holl et al. 2000). In the Neotropics, 75% of rainforest tree and shrub species depend on frugivorous vertebrates for dispersal. But many frugivorous birds and bats avoid large open areas that could expose them to predators (Gunter et al. 2007). Thus, soil seed banks of cleared forests generally become depleted of forest components, either by herbivory, predation, or because seedlings die and are not replaced by primary forest dispersers. Emergence of tree seedlings can be as much as 20 times lower in abandoned pasture than in forest understory (Guevara et al. 1992; Nepsted et al. 1996).

Thus, rather than being viewed as “the living dead” as they were several decades ago (Janzen 1971), remnant trees in pastures are now considered important landscape elements that extend the rate of relaxation (time needed for a community to shift to a new community following species extinction) without expensive management efforts (Brooks et al. 1999). Relict trees in pastures function as regeneration foci because they modify the microclimate of pastures by increasing shade, reducing water stress, and reducing photoinhibition of plants under their

crowns, which enhances survival and growth of saplings beneath them (Holl et al. 2000; Carpenter et al. 2004) and because they provide perching and roosting sites for frugivorous vertebrates. This promotes seed exchange between pastures and surrounding forests (Harvey et al. 2006).

Most plants growing under relict tree canopies are components of the original vegetation rather than pasture species (Guevara et al. 1992; Nepsted et al. 1996). These effects persist even after secondary forests grow up around remnant trees (Schlawin & Zahawi 2008) and have been documented in many habitats. In the Pacific Northwest, isolated "seed trees" in plantations of western larch (*Larix occidentalis*) provide propagules of *Bryoria*, an arboreal lichen that provides critical winter forage for ungulates, for surrounding trees (Bunnell et al. 2007). In tropical pastures, lizards experience a faunal recovery that is linked to the growth of small trees, which provide perches and cover (Glor et al. 2001).

Here we suggest another way relict trees may enhance pasture recovery. In some habitats, remnant trees sustain a seed bank contained within canopy-held soil that accumulates beneath epiphytes, which could augment the availability in pastures of seeds of primary forest trees. These "canopy mats" (carpets of live vascular and nonvascular epiphytes and the canopy soil that accumulates on trunks and the upper surfaces of large branches) occur most abundantly in tropical montane forests (Hofstede et al. 1993), lowland tropical forests (Cardelús & Chazdon 2005), temperate wet forests (Wardle et al. 2003), and coastal redwood forests (Enloe et al. 2006). Canopy soils are created from dead and decomposed epiphytes, animal frass, decomposing bark, crown humus (decomposed amorphous organic matter), and moisture and nutrients from precipitation, and can accumulate up to 44 t/ha. They share similar nutrient content with the upper horizons of the forest floor, but generally have higher organic content, greater cation exchange and water retention capacity, and lower pH (Nadkarni et al. 2004).

Canopy soils in tropical and temperate wet forests also store abundant and diverse plant propagules. A study in Monteverde on the potential effects of climate change on canopy mats in forest and pasture trees revealed that viable seeds of 37 taxa of both arboreal and terrestrial plants are "buried" and retained in the canopy soil in primary forest trees (Nadkarni & Solano 2002). Field experiments showed that seeds stored in canopy mats readily germinated when exposed to the hotter, drier conditions of pasture tree canopies into which they had been transplanted. When the vascular epiphytes of primary forest canopy mats were clipped to remove shade imposed by their foliage, numerous seedlings of terrestrial taxa that were stored in the seed bank germinated and grew up to 80 cm in height.

Because regeneration dynamics of many tropical forests are based on small-gap regeneration, seeds stored

in canopy soils are optimally positioned to be deposited directly into forest tree-fall gaps, locations that favor germination and survival. For example, in Monteverde, the seedlings of some shade-intolerant trees commonly start their lives as epiphytes and then "ride down" branch and tree falls, arriving in the gap created by the parent tree. With a little reorientation, they establish themselves on the forest floor. Thus, in the primary forest, the canopy-held seed bank is part of an unusual and effective form of advance regeneration (Lawton & Putz 1988).

Might this phenomenon also occur in pasture remnant trees? The biology of tree canopies in agricultural settings is poorly documented. The few studies of tree canopies in secondary forests and plantations document that canopy plant communities are generally depauperate in species and low in biomass because of lack of time to accumulate epiphytes, the drier microclimate, and potential differences between pasture and forest tree bark (Heitz-Seifert et al. 1995). Nevertheless, some pasture relict trees retain a legacy of epiphytes and canopy soils from their original habitats for many decades (Flores-Palacio & Garcia-Franco 2004; Wolf 2005).

We propose that the seed bank in pasture canopy soils may function as a "time capsule" of primary forest propagules. Canopy seed banks in pasture relict trees could provide seeds to the current generation from sources that are distant in both time and space, thus enhancing regeneration capacity and planning and implementation of restoration strategies. Here we explored how canopy seed banks compare in pasture and primary forest habitats and whether propagules in the seed bank are viable in the canopy mats.

Methods

Study Site

The Monteverde area in the Cordillera de Tilarán is characterized by a patchwork of primary and secondary forests, coffee farms, pastures containing remnant primary forest trees, and ecotourism facilities (Harvey & Haber 1999). The ecology and agricultural history is well documented (Nadkarni & Wheelwright 2000). The site is on the Pacific slope near the Continental Divide, in the lower montane wet forest life zone, and receives approximately 2500 mm/year of rainfall and 1000 mm precipitation in the form of wind-driven cloud and mist (Clark et al. 1998). Primary forest within the Monteverde Cloud Forest Preserve (MCFP) has been protected for >60 years and has received minimal direct human disturbance during the past several centuries. The forest has a complex structure, with a 25- to 35-m canopy that supports abundant and diverse epiphyte communities. Fieldwork took place in the research area of the MCFP and adjacent pastures (10°20'N, 84°45'W; 1430–1490 m asl) between January 1998 and December 2000. Pastures,

owned by local farmers, were established 60–80 years ago and were composed of low grasses, dominated by the introduced Kikuyu grass (*Pennisetum clandestinum*) and East African star grass (estrella, *Cynodon nlemfuensis*) (Griffith et al. 2000). All pastures contained numerous remnant trees with isolated crowns, with a mean density of 25 trees/ha (Harvey & Haber 1999).

Tree Selection, Canopy Access, and Seed-Bank Sampling

Study trees were selected based on the ability to safely gain access to their crowns with single-rope techniques. Nine forest trees were selected from a pool of trees that had been climbed for previous canopy studies (Nadkarni et al. 2002). All were 60–120 cm diameter at breast height (dbh), 23–34 m in height, and supported thick accumulations of canopy soils (5–20 cm deep on major branches and trunks). Nine pasture trees of the same size class were randomly selected from the pool of trees isolated in pasture sites.

We sampled seed banks from three habitats: pasture-tree canopy mats (hereafter pasture canopy); primary-forest canopy mats (forest canopy); and primary-forest floor soils (forest floor). We sampled trees of one common tree species (*Ocotea tonduzii*, Lauraceae) to avoid potential effects of the host tree species on canopy-soil characteristics and visitation by potential pollinators and dispersers. Trees in primary forest were at least 300 m from pasture-forest borders, and trees in pastures were a minimum of 200 m from any other tree. We took forest-floor samples from random locations beneath sample trees in primary forest. Forest-floor samples (20 × 15 cm and 10 cm deep) were collected from just below the O horizon.

For each tree, we randomly selected one branch segment in the midcrown to sample which was safely accessible to the climber (1–4 m from the trunk); 25–40 cm in diameter; and at an angle 0–30° from horizontal. From this segment, we clipped and removed live stems and foliage of vascular epiphytes and then cut out and bagged the accompanying canopy soil (20 × 15 cm × 10 cm deep). These samples were air-dried in the laboratory for 1–4 days. Bryophytes, roots, and large pieces of organic debris were removed with sieves, and soils were hand-sorted to extract seeds, which were stored in 75% ethanol.

Plant names and ecological characteristics (growth habit, successional status, pollinator type, and dispersal type) were determined for each taxon from the Monteverde updated (February 2008) plant list (Haber 2000; W. A. H., personal observation) and the Tropicos Project database of the Missouri Botanical Garden (<http://mobot.mobot.org/W3T/Search/vast.html>). Growth habit categories were tree, shrub, epiphyte, and liana. Herbs (<3% of the total) were combined with shrubs. Categories of successional status were

primary forest, forest pioneer, secondary forest, and ruderal. Pollination types were bird, bat or arboreal mammal, insect, and wind. Disperser types were bird, bat, arboreal mammal, and wind. If more than one type was designated, we used the most common (listed first). Species for which pollination and dispersal agents were unknown comprised <5% of the species and were not included in the quantitative analyses. Vouchers of seeds were deposited at the MVCP laboratory. Species names and categorization of species is available (see Supporting Information).

Greenhouse Seed Germination

Between August 1999 and April 2000, we carried out greenhouse studies to quantify germination potential. Earlier studies revealed that when epiphytes die or decline, the terrestrial taxa of their seed banks readily germinate (Nadkarni & Solano 2002). This may be due to removal of the shade that epiphytes cast or to some allelopathic effects of the living epiphytes. To mimic the exposed conditions that might exist in pasture trees, we quantified germination in mats from which epiphytes were clipped (pruned treatment) with that of mats that had epiphytes left intact (control treatment). We collected 26 canopy mats (50 cm long) from branches of the primary-forest study trees that had been collected previously (separate from the samples described earlier). We randomly assigned half the mats ($n = 13$) to the pruned treatment. We clipped the vascular epiphyte foliage and stems and removed as much of the living bryophyte material as possible without disturbing the integrity of the mats. The other 13 mats were left intact (control).

Experiments were conducted in a greenhouse located 1 km down slope from the MCFP. Average maximum and minimum temperatures (temperature recorded every 48 h with a maximum–minimum thermometer) were 25.5 °C (SD 1.82) and 15.0 °C (0.74), respectively. Mean ambient temperature was 19.3 °C (1.03). Plants were laid in flats on tables in random order and watered with through-fall from the forest with an automatic misting system for 5 min twice each day. Every 6–8 weeks, emerging seedlings were counted and identified when possible. This interval may have allowed some seeds to sprout and then succumb to herbivory or damping off, so the numbers reported are probably an underestimate of the actual germination percentage. Some taxa were not identifiable but could be distinguished as separate taxa, and were included in the tally of species diversity.

Statistical Analyses

For variables that were normally distributed, we used t tests and one-way analysis of variance (ANOVA) to compare means. The distribution of seed density in samples was not normal, so we used Kruskal–Wallis and Mann–Whitney U tests. We used a G test to analyze the

distribution of seeds among growth habit, successional status, pollination, and dispersal guilds. To assess differences in the entire plant community represented in the seed banks, we used a relativized (to species maximum) nonmetric multidimensional scaling (NMS) ordination with a Sorenson (Bray-Curtis) distance measure in PC-ORD (Version 4.34, McCune & Mefford 1999). Differences among groups were determined with multiresponse permutation procedures (MRPP). We used indicator species analysis to identify species that differentiated among particular habitats.

Results

Abundance and Composition of Seed Bank

A total of 5211 seeds were collected and processed from the three habitats: pasture canopy (1741); forest canopy (1041), and forest floor (2429). The density of seeds in the seed bank of these habitats showed high variability, ranging from 2.3 seeds/dm³ to 203.7 seeds/dm³. Mean density differed significantly among the habitats (Kruskal-Wallis test, $H = 249.01$; $p < 0.001$) (Table 1). Nevertheless, neither seed density of the pasture canopies nor seed density of the forest floor significantly differed from the forest canopies (Mann-Whitney test, $U = 63$ and 61 , respectively; $p < 0.01$).

Eight species in 44 families and 61 genera from all of the habitats were tallied. There were 37 species in the pasture canopy, 33 in the forest canopy, and 57 in the forest floor (Table 1). The mean species richness (number of species per sample) was significantly greater on the forest floor than either the forest canopy or pasture canopy (Table 1; $F = 83.38$; $p < 0.001$, one-way ANOVA). The mean species richness in the pasture canopy was significantly higher than the forest canopy ($t = 2.33$; $p < 0.02$). There were no differences in species diversity (Simpson's index) between pasture-canopy and forest-canopy samples ($t = 1.20$; $p = 0.09$) or between forest-canopy and forest-floor habitats ($t = 1.48$; $p = 0.10$) (Table 1). Nevertheless, there was a significant effect of habitat when all habitats were compared ($F = 4.02$; $p < 0.02$). A similar number of species overlapped between the three pairs of habitats (pasture canopy [PC]/ forest canopy [FC]: 14 species; forest canopy/forest floor [FF]: 19; forest floor/pasture

canopy:21). There were 11 species (13% of the total) held in common in all three habitats.

All habitats were dominated by a relatively small number of plant families. The five most common families made up a large proportion of the total: 82, 92, and 86% of pasture canopy, forest canopy, and forest floor, respectively. Moraceae and Solanaceae were present as the most common families in all three habitats. Cercropiaceae and Moraceae were the most common families in forest canopy and forest floor. Each habitat had at least two unique families (PC, Araliaceae, Myrsinaceae, and Rosaceae; FC, Asteraceae and Ericaceae; and FF, Euphorbiaceae and Urticaceae).

At the species level, a small number of species made up a very large proportion of the total diversity, which was reflected in steep dominance-diversity curves (Fig. 1). Species in forest canopy and forest pasture had a slightly more geometric distribution, representing the dominance of a few species, which is characteristic of harsh or marginal environments. The forest floor has a more lognormal distribution with relatively high equitability. Species evenness was slightly higher in the forest ground than either arboreal community, as indicated by its slightly flatter curve. The three dominant species in the pasture canopy (*Myrsine coriacea*, *Rubus rosifolius*, and *Oreopanax oerstediana*) were not the most common species in the forest-canopy or forest-floor habitats. The latter had the same most common species (*Cecropia polyphlebia*, *Lycianthes synathera*, and *Ficus tuerckheimii*) as the forest canopy.

In terms of community composition in general, seed banks in pasture canopy, forest canopy, and forest floor were significantly distinct from one another ($A = 0.273$; $p < 0.0001$). Seed-bank communities also differed significantly between pasture canopy and forest canopy ($A = 0.208$; $p < 0.00003$) and between forest canopy and forest floor ($A = 0.1458$; $p < 0.0003$). Twenty-one species were indicators of a particular habitat ($p < 0.03$; Supporting Information). Most of these were for the forest floor.

Plant Forms and Guilds

The distribution of species in the four growth forms did not differ significantly overall ($G = 11.5$; $p = 0.07$) or between the pasture canopy and forest canopy habitats

Table 1. Seed characteristics of soil samples collected from the forest floor and from canopies of trees in pasture and forest.

	Pasture canopy	Forest canopy	Forest floor
Mean no. of seeds/dm ³ (SD)	64.5 (54.8)	38.6 (60.5)	86.4 (34.7)
Total number of species	37	33	56
Mean number of species (SD)	4.7 (1.8)	2.7 (1.8)	6.8 (1.1)
Species richness (SD)	14.1 (5.3)	8.2 (5.4)	20.4 (3.8)
Species diversity (SD)*	0.465 (0.682)	0.580 (0.232)	0.709 (0.118)

*Simpson's index.

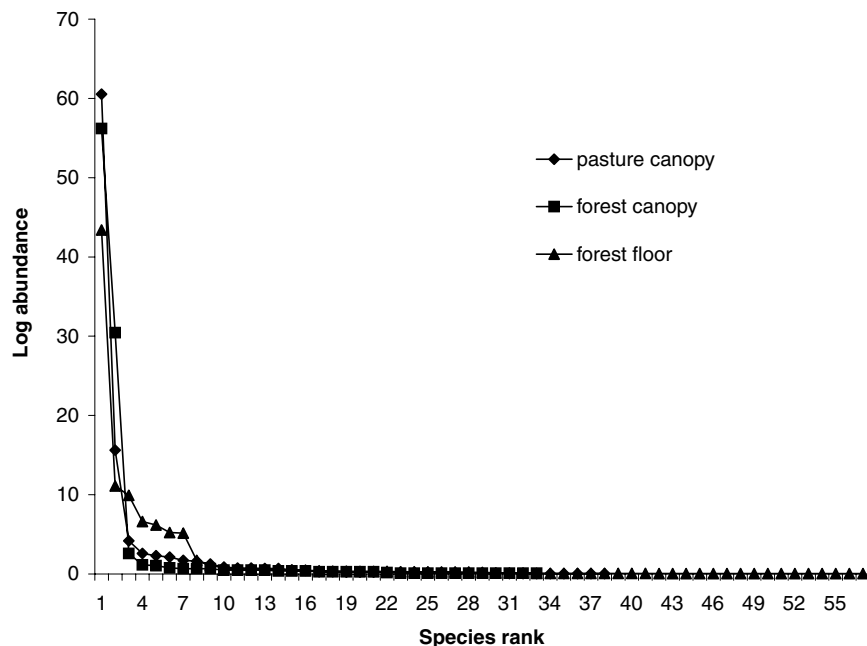


Figure 1. A dominance-diversity plot for the distribution of taxa of seeds sampled from the pasture canopy (PC), forest canopy (FC), and forest floor (FF).

($G = 4.73$; $p = 0.192$) (Fig. 2). Nevertheless, for the number of seeds, there was a significant difference in the distribution of growth forms between pasture canopy and forest canopy ($G = 1473.30$; $p < 0.001$). There was

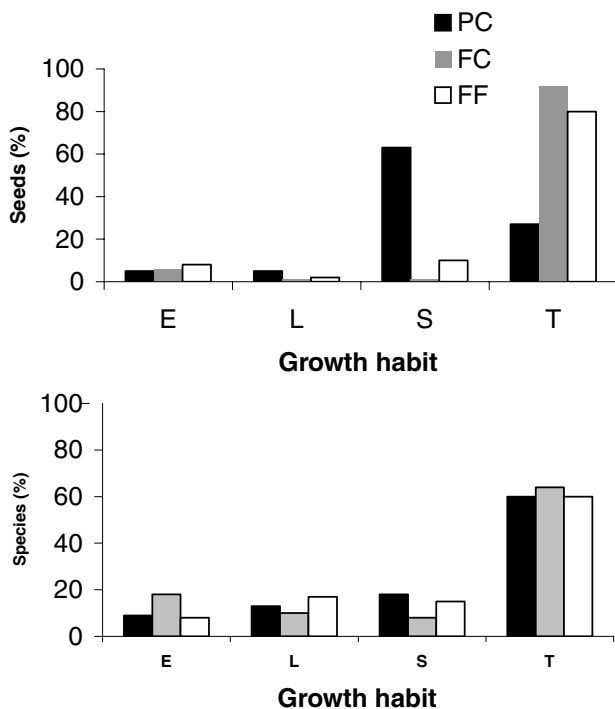


Figure 2. Distribution of seeds in growth-habit categories (E, epiphytes; L, lianas; S, shrubs and herbs; T, trees) in the three habitats: pasture canopy (PC), forest canopy (FC), and forest floor (FF). Distributions were calculated from proportion of seeds (top) and proportion of species (bottom).

one highly dominant species (by number of seeds) in the pasture canopy soils, *R. rosifolius*, but even after removal of this species from calculations, there was a significant difference in seed density between pasture canopy and forest canopy (G test = 177.78; $p < 0.00001$). For all three habitats, about 10% of the species were canopy-dwelling plants (8.9, 10.0, and 11.1% of the pasture canopy, forest canopy, and forest floor, respectively). Thus, both terrestrial- and canopy-plant propagules were represented similarly. The three habitats did not differ overall in terms of proportion of plants of different successional status ($G = 5.17$; $p = 0.522$); primary forest and forest pioneer seeds dominated in all three habitats. Less than 20% of species were ruderals (Fig. 3).

There were no differences in proportion of species of different pollinating syndromes among habitats ($G = 4.97$; $p = 0.547$) or between the forest and pasture canopies ($G = 1.05$; $p = 0.788$). Nevertheless, the number of seeds in forest and pasture canopies differed significantly ($G = 710.82$; $p < 0.000001$) with and without *R. rosifolius* (Fig. 4). Dispersal types followed the same pattern (Fig. 5); species of seeds among the dispersal guilds did not differ overall ($G = 2.03$; $p = 0.916$) or between pasture and forest canopy ($G = 1.51$; $p = 0.679$), but did differ significantly in seed density ($G = 1245.32$; $p < 0.00001$).

Germination Experiments

A total of 2488 seedlings emerged from the experimental mats in the greenhouse. Twenty-eight taxa germinated: 23 in the pruned mats, 16 in controls, and 10 that occurred in both treatments. Seven of the taxa could not be identified. Of all of the seeds, 80% (2000) sprouted

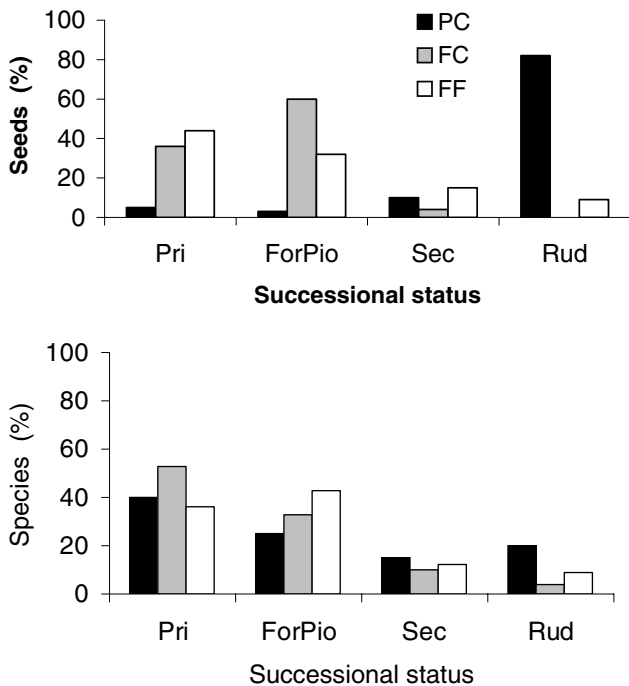


Figure 3. Distribution of seeds by successional stage (Pri, primary; ForPio, forest pioneer; Sec, secondary; Rud, ruderal) in the three habitats: pasture canopy (PC), forest canopy (FC), and forest floor (FF). Distributions were calculated as proportion of species of seeds.

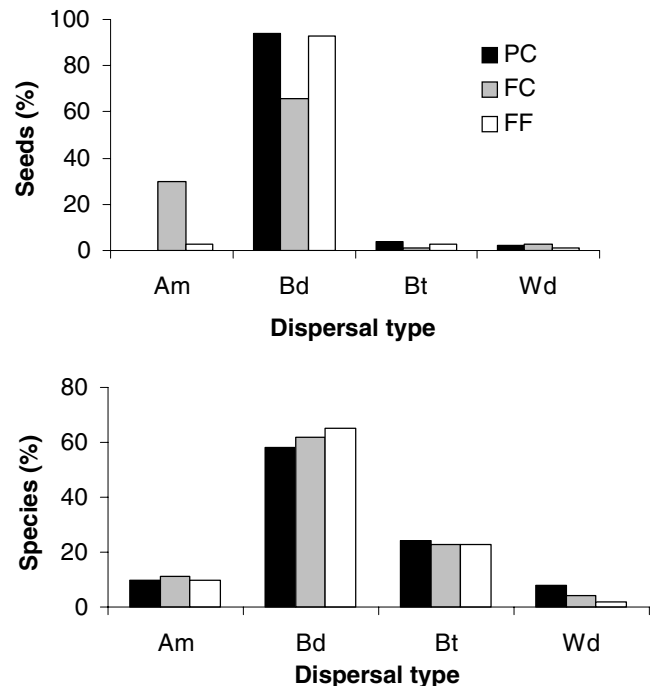


Figure 5. Distribution of seeds by dispersal type (Am, arboreal mammal; Bd, bird; Bt, bat; Wd, wind) in the three habitats: pasture canopy (PC), forest canopy (FC), and forest floor (FF). Distributions were calculated from both proportions of seeds (top) and species (bottom).

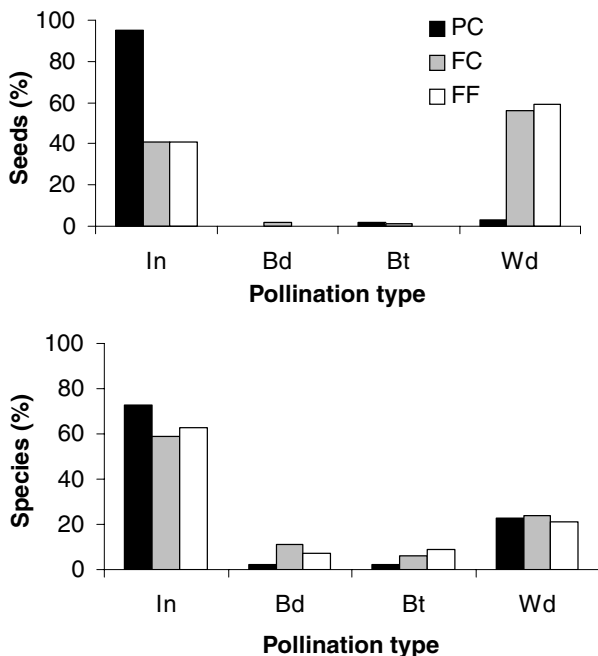


Figure 4. Distribution of seeds by pollination type (Bd, bird; Bt, bat; In, insect; Wd, wind) in the three habitats: pasture canopy (PC), forest canopy (FC), and forest floor (FF). Distributions are calculated from both proportions of seeds (top) and species (bottom).

from the pruned mats, indicating that the more exposed conditions were more conducive to germination than the intact mats (controls). All taxa that sprouted from the experimental mats were present as seeds in the samples taken from previously sampled seed-bank canopy mats. The dominance-diversity curves of the two treatments were similar in shape, indicating dominance by a relatively small number of taxa, with many rare species. Nevertheless, the relative proportion of taxa differed between seeds and seedlings. In the pruned treatment, the three most common taxa (55% of all seedlings) were *Conostegia oerstediana*, *C. polyphlebia*, and *Piper* sp., none of which was among the most common species in the pasture canopy, but *C. polyphlebia* was among the three most common species in the forest canopy.

The seedlings that germinated were from all four growth forms and all four successional status types (Table 2). Nearly half (48%) of the seedlings were trees, 24% were shrubs, 19% were epiphytes, and 5% were lianas. Secondary species comprised 43% of the seedlings; relatively few ruderal species (10%) were present. Nearly half the species were undisturbed-forest species (primary forest, 19%; forest pioneer stage, 29%).

Table 2. Family and taxon of seedlings that emerged from seed-bank samples in the greenhouse study.*

Family	Taxon	Growth habit	Successional status
Aracaceae	<i>Anthurium pittieri</i>	L	FORPIO
Asteraceae	<i>Senecio cooperi</i>	S	SEC
Asteraceae	<i>Neomirandea angularis</i>	E	FORPIO
Begoniaceae	<i>Begonia</i> sp.	S	SEC
Celastraceae	<i>Perrottetia longistylis</i>	T	FORPIO
Clusiaceae	<i>Clusia stenophylla</i>	T	PRI
Euphorbiaceae	<i>Sapium glandulosa</i>	T	FORPIO
Gesneriaceae	<i>Columnea</i> sp.	E	PRI
Melastomataceae	<i>Conostegia oerstediana</i>	T	SEC
Melastomataceae	<i>Blakea</i> sp.	E	SEC
Moraceae	<i>Ficus tuerckheimii</i>	T	PRI
Moraceae	<i>Cecropia polyplebia</i>	S	SEC
Myrsinaceae	<i>Ardisia palmana</i>	T	SEC
Phytolaccaceae	<i>Phytolacca rivinoides</i>	S	RUD
Piperaceae	<i>Piper</i> sp.	S	SEC
Rubiaceae	<i>Guettarda poasana</i>	T	FORPIO
Solanaceae	<i>Solanum aphyodendron</i>	T	SEC
Solanaceae	<i>Lysianthes synanthera</i>	E	PRI
Solanaceae	<i>S. umbellatum</i>	S	RUD
Ulmaceae	<i>Trema micrantha</i>	T	SEC
Urticaceae	<i>Urera elata</i>	T	FORPIO

*Seedlings were classified into habit (tree, T; shrub and herb, S; epiphyte, E; and liana, L); successional stage (primary forest, PRI; forest pioneer, FORPIO; secondary forest, SEC; and ruderal, RUD). Placement of taxa into categories is modified from Haber (2000) and W. A. H. (personal observation). Seven taxa could not be identified.

Discussion

Seed-bank densities and diversities were consistent with those in terrestrial soils in other montane forests and pastures (Harvey 2000). No previous reports exist on the content or significance of pasture-canopy seed banks in tropical landscapes. These results show that the abundant and diverse seed banks that exist in the crowns of isolated pasture trees are on a par with those in the forest canopy and that pasture trees had slightly lower diversity and densities than forest-floor seed banks. Although the community composition of the pasture- and forest-canopy seed banks differed overall, they shared many taxa at the family, genus, and species levels. Most important, pasture-canopy seed banks harbored many viable primary-forest taxa that are animal-pollinated and animal-dispersed, which is in contrast to past findings that regeneration of woody plants is limited in pastures (Aide et al. 1995). These pasture-canopy seed banks share some similarities with traditional canopy seed banks (i.e., propagules stored in serotinous cones of conifers [Daskalakou & Thanos 1996]) in which seeds are held in canopy cones for varying periods of time and then released when conditions favor germination.

The greenhouse and germination study showed that nearly half the species that germinated from the mats were trees, and over 40% of these species were primary forest or forest pioneer species. This supports the idea that canopy mats may function as time capsules because

they store viable seeds that are not ruderal and provide a perching point for dispersers of secondary species that arrive at locations where such propagules are lacking. In addition, because of where they will ultimately fall (in the shade of the host tree), the fallen seeds and their accompanying nutrient-rich mats may provide an advantage in terms of pasture regeneration. In habitats such as open pastures, falling in the shade of a tree may constitute an advantage because reduced insolation helps maintain water balance of young seedlings (Sampaio et al. 2007).

These results are relevant to management practices in agricultural landscapes. Human activities to elevate seed dispersal, such as planting native tree seedlings to increase canopy architecture, installing bird perches, and artificially establishing shrubs have met with mixed results (Harvey et al. 2008). In a montane pasture in Costa Rica, for example, crossbar perches in the open resulted in a slightly elevated below-perch seed rain density, but bird visitation rates were low and few of the species were frugivores or forest species (Holl 1998).

How might real pasture-canopy seed banks function to enhance pasture recovery? Epiphyte mats and their accompanying primary forest seeds in pasture trees can be dislodged by arboreal mammals, branches may fall, or the whole tree may topple to the ground. There, seeds gain access to soil and sufficient light and shade to survive and grow. When canopy mats in the primary forest fall to the ground, they go through "moss meltdown." Within 2 months, epiphytic plants die and decompose, leaving

clumps of exposed, dead organic matter. Seedlings of vascular plants (epiphytes and terrestrial seedlings from the canopy seed bank) then sprout from the fallen mats (Matelson et al. 1993), which indicates these mats may function as woody-plant nurseries on the forest floor. Documenting the fate of canopy seed banks in pastures was beyond the scope of this study, but further work could follow germination ecology of mats through observation or experimentation.

Other questions stem from this study: How will the composition of canopy seed banks change over time as the original species get diluted through germination or herbivory and as they are augmented by pollinators and dispersers that visit from the primary forest? Will these seeds ultimately augment the population of pasture's terrestrial trees, or will they die in the face of exposed pasture conditions, soil compaction, herbivory, and predation? Answers to these questions are critical to predicting how pasture seed banks will serve as repositories of propagules for the next generation of trees in pastures. With increasing threats to biodiversity and ecosystem function that come from primary-forest loss, fragmentation, and conversion, this source of time-capsule seeds from the forest should be considered by conservationists and managers concerned with accelerating pasture recovery.

Acknowledgments

We thank R. Solano for field assistance and identification of seeds. T. Matelson and N. Lecomte helped with analysis and ecological insights. The Missouri Botanical Garden provided support for aspects of plant taxonomy. G. Murray provided access to seed vouchers and to his greenhouse. C. LeRoy helped greatly with the ordination analyses. We thank the Monteverde community, particularly W. and L. Guindon, J. and D. Campbell, and G. Powell for access to pastures. The MVCP and the Centro Científico Tropical protects the primary forest site. The National Science Foundation provided an OPUS (Opportunities to Promote Understanding through Synthesis, DEB 05-42130) and other grants (DEB-9974035, DEB-9975510, BDEI 0417311). The Helen R. Whiteley Center provided support for synthesis of this research. We thank two anonymous reviewers for their helpful comments on the draft manuscript.

Supporting Information

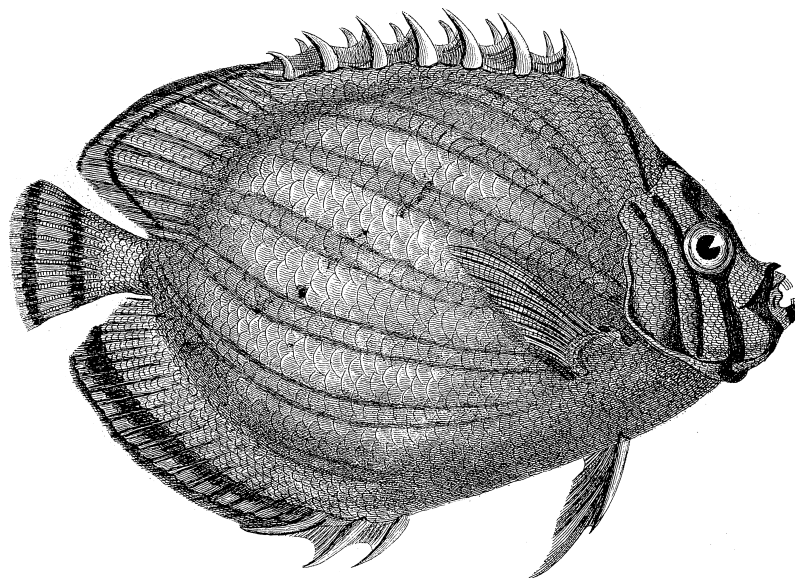
Seed taxa sampled (Appendix S1) and indicator species (Appendix S2) lists are available as part of the on-line article. The author is responsible for the content and functionality of these materials. Queries (other than absence

of the material) should be directed to the corresponding author.

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Cover: Tropical pastures present multiple barriers to tree regeneration, but canopies of relict trees can serve as repositories of viable seeds deposited when the forest was intact. When mats of arboreal soil fall to the pasture floor, their seedbank can contribute to forest regeneration, their seeds serving as “time capsules” from the primary forest. The lush epiphytic ferns (*Polypodium* spp.) and accompanying arboreal soil on this mature live oak are viewed from above in a subtropical landscape of Florida. Photo by John T. Longino. See pages 1117–1126.

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