RESEARCH ARTICLE

Floristics of soil seed banks on agricultural and disturbed land cleared of tropical forests

Madhushi Weerasinghe[1], Mark S. Ashton[2,3] , Elaine R. Hooper[2], Balangoda M. P. Singhakumara[1]

Little is known about how soil seed banks vary in germination, composition, and density under different land uses after tropical forest conversion. Seed banks can potentially act as one source of regeneration for reforestation of old agricultural lands. Our study documents the composition and density of germinants in soil seed banks from four land uses types surrounding the Sinharaja forest in southwest Sri Lanka. These include: (1) kekilla fern lands; (2) pine plantations; and (3) tea. These were compared to the adjacent (4) mature rainforest. During the 6-month period of monitoring, we recorded 1,674 germinants (0.036 germinants/cm^3 soil), representing 46 species. Germinants of tree and shrub species were restricted to the pine and rainforest soils and all of them are considered pioneers. The soils of the rainforest had the lowest species richness, density, and diversity of germinants; tea lands comprised much higher richness, Shannon diversity, and density. However, almost all germinants in tea were grasses and herbs as compared with other land uses. A multivariate analysis of the germinants of soil seed banks revealed that the four land use types comprise very different compositions and abundances, some of which can be associated with differences in growth habit (trees, shrubs, vines, herbs, grasses). Our results suggest that pine plantations may facilitate some tree and shrub regeneration. However, the seed banks beneath tea and kekilla fern land do not comprise any woody plant species. This may explain why agricultural lands such as tea do not revert back to forest easily.

Key words: degraded, land use, pioneers, regeneration, restoration, seed bank, seedlings, Sinharaja

Implications for Practice

- Tea lands comprise soil seed banks that only contain herbs and grasses, suggesting that they cannot easily revert back to native second-growth forest after abandonment but instead need to be planted if reforestation is a desired outcome.
- Pine plantations on former tea land comprise seed banks that include both pioneer shrubs and trees that may facilitate the establishment of second-growth native forest.

Introduction

Increasing population, land clearance for agriculture, and industrial timber logging are some of the complex and interacting causes of tropical rainforest loss and conversion to other land uses (Chen et al. 2013). Many of these lands are subsequently abandoned and questions arise as to their capacity to reforest spontaneously (Bai et al. 2008). Over 100 million hectares of former tropical forest lands in Asia now face degradation and this has resulted in a demand for policies on their restoration by both government and nongovernment organizations (van Lynden & Odeman 1998; Bai et al. 2008). Seeds from nearby forest fragments, seed dispersed by wind, birds, and bats, and residual surviving plants are the major sources of potential revegetation of cleared forest areas (Devendra 1997; Ashton et al. 2001; Guariguata & Ostertag 2001). One other source is seed that resides in the soil either from when the forest was originally cleared, or from seed rain dispersed by wind or animals that has accumulated in the soil over the years following land clearance. These seeds can remain dormant for a long period of time and constitute the "soil seed bank" (Vázquez-Yanes & Orozco-Segovia 1993; Fenner & Thompson 2005).

Seed banks may be either transient, with seeds that germinate almost immediately, or persistent, with seeds that remain in the soil for many years (Leck et al. 1989). A seed bank can only function if seeds in it retain their viability as sources of potential revegetation on cleared and open areas. Evidence of extreme longevity in seeds has been recorded from archeological and paleoecological sites (Van Der et al. 2009; Cappers & Neef 2012), from dated herbarium sheets (Bowles et al. 1993), and from a variety of field experiments (Leck et al. 1989; Singhakumara et al. 2000). When seeds in soil seed banks are exposed to light, increased temperature, and moisture, or some combination

of these environmental factors, dormancy is broken and germination is triggered (Vázquez-Yanes & Orozco-Segovia 1993; Devendra 1997). Soil seed banks potentially play a major role in the establishment and development of secondary succession, and studies on these processes are considered a necessary first step for the design of plans for ecological restoration (Bossuyt & Honnay 2008).

Some studies support the idea that seed banks can play an important role in local diversity maintenance through temporal storage effects that, upon seed germination and release, can help maintain or promote functional attributes of ecosystem recovery (Luzuriaga et al. 2005; Mall & Singh 2014); but others conclude that they have little potential for restoration of natural ecosystems (Mall & Singh 2014). Many of the studies concluding that soil seed banks had little potential for revegetation examined the role soil seed banks play within intact tropical rainforests. Results reported lower species richness and a higher percentage of early-successional pioneer tree species relative to the original vegetation (Hopkins & Graham 1983; Bekker et al. 2000). Most of these studies were conducted within rainforests of the Neotropics. Findings in Barro Colorado, Panama suggest that though pioneers make up the majority of tree species found in soil seed banks of intact tropical forests, they show dramatic spatial variation associated with the presence or absence of fruiting pioneers within canopy gaps (Dalling et al. 1998). Other studies in Puerto Rico have shown the effect of edge with a dramatic decrease in the seed bank the further away from the forest with over 50% represented by one pioneer tree *Trema lamarckianum* (Cubiña & Aide 2001).

Studies of old fields and second-growth forest seed banks in Mexico and Costa Rica show that early-successional herbs and shrubs dominate. Species richness of a seed bank in second-growth rainforest at La Selva, Costa Rica was estimated to be 36 (Butler & Chazdon 1998) while for second-growth forest in the Yucatan, Mexico between 42 and 65 species were recorded (Rico-Gray & García-Franco 1992). For second-growth forest in Chiapas, Mexico up to 130 species were identified, with between 32 and 52 species identified per disturbed forest site of which 25 early-successional species made up 70% of the germinants (Quintana-Ascencio et al. 1996). Studies elsewhere investigating seed banks show the same trends. For example, both fragmented rainforests of the Brazilian Atlantic region (Martins & Engel 2007) and land conversion to agriculture of dry Afromontane forests in Ethiopia (Teketay 1997) comprised a seed bank diversity largely of early-successional herbs and shrubs. For the Brazilian Atlantic region, though nonwoody taxa predominated in fragmented forest, pioneer tree species were better represented in the less disturbed forest (Martins & Engel 2007).

Soil seed bank studies in tropical forests of Asia have largely been confined to the role they potentially play within intact mature tropical forests. Most studies demonstrate that in undisturbed tropical forests of the Far East the buried seed bank density and number of species are low (Metcalf & Turner 1998; Singhakumara et al. 2000). A study in the Western Ghats by Chandrashekara and Ramakrishnan (1993) found that soil seed density beneath recent canopy openings of a primary rainforest

was low, but older gaps comprised increased soil seed densities. In addition, the proportion of late-successional and pioneer species differed with a greater proportion representing pioneer shrubs and herbs in younger gaps than old ones. Other studies have demonstrated that invasive species have become dominant in Asian rainforests, replacing native species in soil seed banks. For instance several exotics from South America now dominate intact rainforest soil seed banks in South and Southeast Asia, and in Australasia (e.g. *Mimosa pigra* in northern Australia—Lonsdale et al. 1988; *Piper aduncum* in Papua New Guinea—Rogers & Hartemink 2000; *Clidemia hirta* in Sri Lanka—Singhakumara et al. 2000).

No studies that we are aware of have investigated the role that seed banks can potentially play in reforestation of disturbed lands within tropical Asia. The reason for embarking on our study was to investigate the species composition and restoration potential of soil seed banks contained within actively disturbed and abandoned agricultural lands for passive reforestation. In Sri Lanka and South India, many private tea lands that were formerly forest can now no longer sustain tea and have reverted to ferns (Sohng et al. 2017). Similarly, public protected lands illegally cleared of native forest for tea cultivation have also reverted to ferns and grasses. Their restoration to forest for watershed protection, biodiversity conservation, and increased productivity of other forest-based crops is therefore important. We aim to document the variation in the density and species composition of germinants in soil seed banks in relation to different land use types that include (1) pine plantations; (2) tea lands; and (3) kekilla fern (*Dicranopteris linearis*) lands, and compare these land use types with the adjacent intact rainforest. No such studies have yet been done in tropical Asia on the role soil seed banks play in disturbed and agricultural land. Our results provide critical baseline data for the potential for understanding under what circumstances, if desired, passive reforestation can be undertaken.

Methods

Site Description

Sinharaja Forest is the least disturbed and most biologically unique lowland rainforest now remaining in Sri Lanka (Gunatilleke 2004). Industrial logging was carried out from 1971 until 1977 in the Sinharaja Forest but was banned due to public pressure. It was declared a Man and the Biosphere Reserve in 1985 and later a UNESCO World Heritage Site in 1988. This forest covers an area of approximately 11,187 ha and is situated in the southwest lowland wet zone of Sri Lanka within the Sabaragamuwa and southern provinces, latitudes 6°21′–6°26′N and longitudes 80°21′–80°26′W. The elevation of the Sinharaja region of our study site ranges from 300 to 500 m.

Annual rainfall and the mean temperature ranges between 3,750 and 6,000 mm and 25–27°C, respectively. Rainfall is distributed relatively evenly throughout the year but can fluctuate, with a minimum of 200 mm in February and a maximum occurring during the southwest (May–July; recorded maximum is

2,000 mm in May) and northeast (October–January) monsoonal periods (Ashton et al. 1997; Gunatilleke 2004). Soils are classified as Ultisols (USDA 1975; Panabokke 1996); they are located on ridge and valley topography underlain by metamorphic schist and gneiss (Cooray 1984).

In the periphery of the Sinharaja Forest, substantial areas of the rainforest are partially degraded and fragmented due to timber extraction, human encroachment, and conversion to agriculture. Most of these activities were stopped approximately 30 years ago. The buffer of the forest now represents a mosaic of several land uses that comprise Caribbean pine (*Pinus caribaea*) plantations, village home gardens, and tea plantations; some of these areas are covered with secondary scrub and kekilla fern lands. We used four of these land use types in the present study, intact rainforest, and three disturbed and agricultural land uses; these land use types are detailed below.

Forest. We utilized intact primary rainforest within the Sinharaja Forest. This forest type has been well described as a mixed dipterocarp forest comprising approximately 250 late-successional tree and shrub species dominated by the tree family Dipterocarpaceae (Gunatilleke 2004).

Kekilla land. Kekilla lands are covered with kekilla fern (*Dicranopteris linearis*), which originated following rainforest clearance in the 1950s, followed by tea plantations which were abandoned 30 years ago. This land use type represents degraded wastelands common across South and Southeast Asia after forest clearance and cultivation failure, and it is widely distributed on open lands. These lands revert to fern lands that are maintained by periodic fires. They are almost completely covered by a mono-dominant thicket of the pan-tropical fern. This fern comprises a 1-m-thick smothering cover of interwoven trailing fronds on top of the ground surface.

Pine plantation. Between 1978 and 1985, the Sri Lankan Forest Department began planting Caribbean pine (*P. caribaea*) on some of the fern lands to establish a live boundary around the Sinharaja reserve. Pine plantations were selected in our study as another important land use because of their potential value as a surrogate to facilitate the release of soil seed banks beneath their canopy as a source of native tree regeneration (Shibayama et al. 2006; Tomimura et al. 2012). The pine plantations were planted on a 2×2−m spacing and after approximately 15 years they shaded out the fern and promoted the establishment of pioneer vegetation in the understory, which comprised approximately 25 tree species, including some original rainforest species (see Shibayama et al. 2006; Tomimura et al. 2012 for a list of species).

Tea. The study area also surrounds the villages of Kudawa and Pitakele, of which about 46–59% of the households have home gardens of 0.1–0.4 ha (Martin et al. unpublished data). Currently, extensive areas surrounding the home gardens are now tea gardens. Over 95% of the villagers cultivate tea (*Camellia sinensis*) as an important source of income (Wijesooriya & Gunatilleke 2003). We selected tea lands as our third land use category to compare with the original forest, given its preeminence as a crop in the region and because tea is the leading cause of rainforest land clearance in southwest Sri Lanka. Such lands are dominated by closely spaced pruned tea bushes intermittently spaced with a variety of shade trees (e.g. *Gliricidia sepium*) and a completely bare ground story of exposed soil.

Soils on kekilla fern lands and tea lands are drier and more basic than forest and pine land because of the more open conditions and the current or legacy application of fertilizer (Sohng et al. 2017).

Experimental Design

Three sites for each land use type (forest, kekilla land, pine plantation, and tea) were selected randomly for the study. Locations of the sites were widely distributed with coordinates taken using GPS (see Table 1; Fig. 1). Soil samples were taken at each site up to the depth of 5 cm, after removing the litter layer and gravel, but including the fine component of the organic layer. Soil samples were taken using a cylinder of 10-cm diameter to insure an equal volume (392.5 cm^3) was sampled across sites and land use types. Ten soil samples were randomly selected from different locations within each site, and in total we collected 120 soil samples (10 samples per site × 3 sites per land use type × 4 land use types = 120). Each sample was individually sealed in a paper bag and taken to the University of Sri Jayewardenepura for laboratory processing and analysis. Processing involved the removal of all roots and large particles. All soil samples were collected in May 2015 during the onset of the southwest monsoon.

In total, 120 plastic germination trays (each 30 cm × 30 cm) were filled halfway with sand that had been sterilized in a drying oven for 24 hours at 100°C. Each soil sample was spread evenly over the sand in a single tray at 0.5 cm thickness to ensure complete germination (Dalling et al. 1995). The trays were kept in a glasshouse at the University of Sri Jayewardenepura, exposed to full sun, and kept moist by daily watering. Additional protection from contamination by outside sources of seed was provided through clear plastic screening that promoted ventilation while allowing approximately 95% of the direct light to pass through. The number of viable seeds in each soil sample was estimated by counting germinants in the soil trays at regular intervals. Trays were reassigned locations randomly once per week inside the glasshouse to reduce the effect of any spatial variations in temperature and light intensity. Monitoring of germination continued over a period of 6 months (02 May, 2015–02 November, 2015). After the 6-month period, all the germinants were removed and soil samples were gently scarified at the surface and kept for another 1-month period until no further germination occurred.

All germinant seedlings were first marked and counted every 5 days. Species identification was done using field experts, plant identification keys (de Vlas & de Vlas de Jomg 2008), and by comparing with specimens of the National Herbarium at Peradeniya. Seedlings that were able to be identified were marked and counted. Unidentified seedlings were pressed and dried for future identification.

Table 1. Distances between sites in meters as measured by GPS points (F, natural forest; K, kekilla fernland; P, pine plantations; T, tea lands) and GPS points (*X,Y*).

| Site		F			P			T			K		
	01	*02*	*03*	*01*	*02*	*03*	*01*	*02*	*03*	*01*	*02*	*03*
F 01	—	187	510	720	702	1,540	127	248	220	60	206	314
02	—	—	336	633	751	1,590	309	283	236	157	233	194
03	—	—	—	386	763	1,560	615	417	401	458	407	198
P 01	—	—	—	—	562	1,260	154	518	543	654	534	434
02	—	—	—	—	—	845	705	475	523	650	523	629
03	—	—	—	—	—	—	1,510	1,380	1,460	1,510	1,310	1,360
T 01	—	—	—	—	—	—	—	318	279	178	279	437
02	—	—	—	—	—	—	—	—	53	189	142	238
03	—	—	—	—	—	—	—	—	—	149	120	208
x	6.4311	6.431	6.4350	6.4376	6.4353	6.4389	6.4303	6.4330	6.4328	6.4316	6.4327	6.4338
y	80.400	80.37	80.398	80.401	80.407	80.414	80.408	80.401	80.407	80.401	80.407	80.392
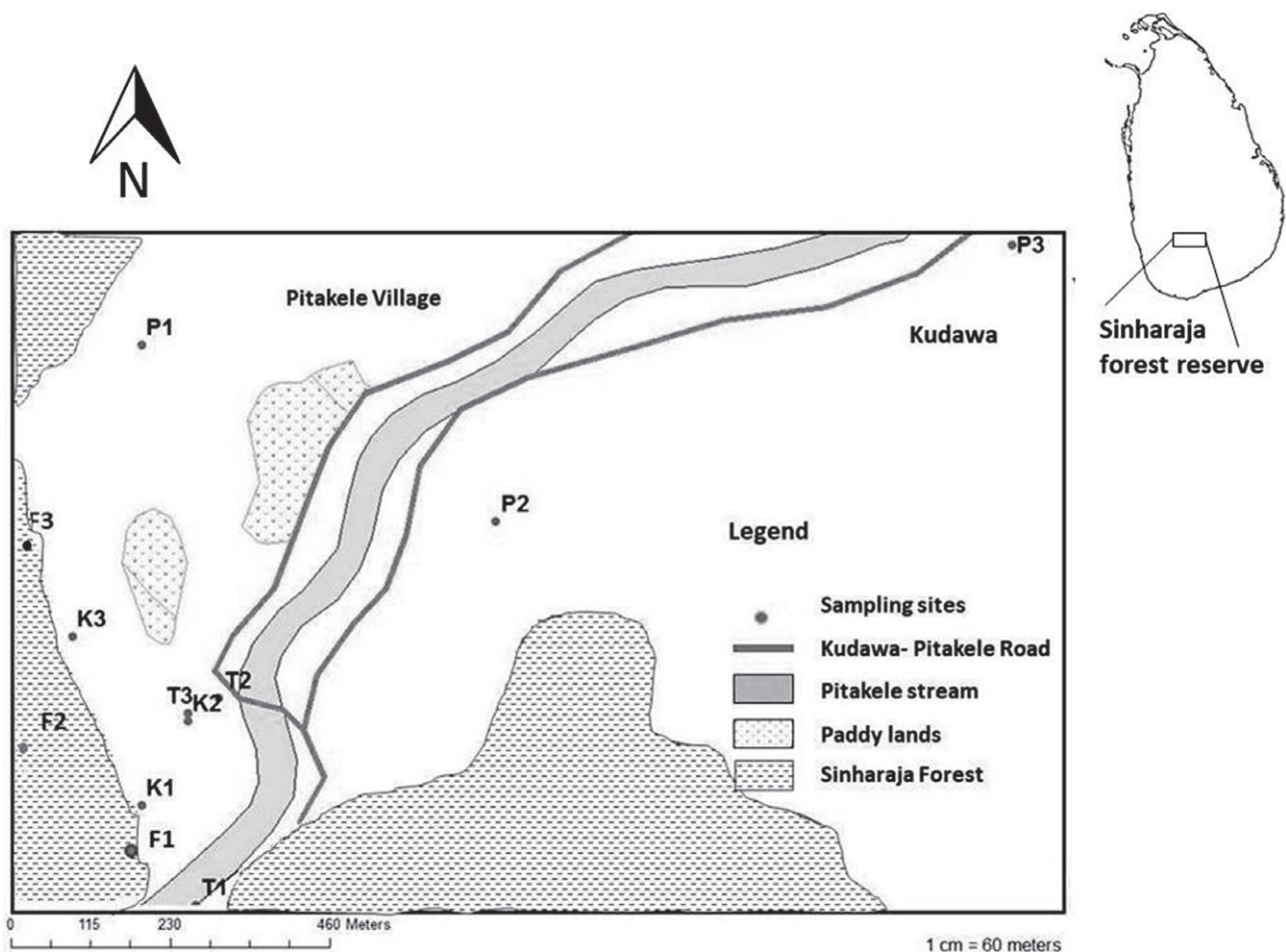
Figure 1. A location map depicting the soil seed bank study sites adjacent the Sinharaja Rain Forest Reserve. F, forest; K, kekilla; P, pine; T, tea.

Data Analysis

We tabulated numbers of germinants by species and land use type (forest, kekilla land, pine plantation, and tea) and calculated percentages by dominant species and growth habit (tree/shrub, vine, herb, and grass) (Table S1). To determine the effect of land use type on our response variables, we used a one-way nested analysis of variance (ANOVA) (sample nested within site). Response variables included species richness, germinant density, and species diversity expressed by the Shannon index. The Shannon or Shannon–Weaver (or Shannon–Wiener) index

is defined as $H' = -\Sigma p_i \ln p_i$, where p_i is the proportional abundance of species i. We used the Shannon diversity index because it is widely used, thus providing comparisons with our study and the literature, and it takes into account the number of individuals as well as the number of species, thus providing more information than simply species richness (i.e. the number of species present). We tested for normality and homogeneity of variance and transformed response variables where appropriate. Tukey post hoc analysis was performed on all variables found to be significantly ($p < 0.05$) affected by the factors.

To determine the effect of land use type on species composition, we used distance-based redundancy analysis (db-RDA) (Legendre & Anderson 1999); the procedure analyzes the effect of experimental factors from an ANOVA model on species community compositional data and allows the use of any dissimilarity measure appropriate for the specific community compositional data at hand. We used two dissimilarity measures: (1) the Jaccard dissimilarity index, which is based on presence/absence data and thus emphasizes the effect of land use type on species identities; and (2) the Bray–Curtis dissimilarity index, which incorporates abundance data and thus emphasizes the effect of land use type on species' relative abundances. Germinants were pooled per site × land use combination (i.e. all 10 samples per site were pooled), and we utilized 99,999 permutations for each db-RDA.

A fourth-corner analysis was performed to evaluate whether species' growth habit (grass, herb, vine, shrub, tree) of soil seed banks are significantly associated with land use type (forest, pine plantation, kekilla land, and tea) as outlined by Legendre et al. (1997); we used model 1 and presence/absence data. The analysis assesses by permutation testing (9,999 permutations) whether the correlations between species' growth habit and land use type are significantly different from the values they would have had in a randomly organized environment using the Pearson's chi-square and G statistic (Legendre et al. 1997).

All statistics were carried out using R 2.11.1 (R Development Core Team 2008, Geneva, Switzerland).

Results

Germinant Floristics

A total of 1,674 germinants were recorded over the 6-month period (0.036 germinants/cm^3 soil), representing 24 families and 46 species (see Table S1). The total density of germinants recorded for the forest, pine, kekilla land, and tea were 0.019, 0.028, 0.045, and 0.051 germinants/cm^3 soil, respectively; or the total germinant numbers recorded of 220 for forest, 324 for pine, 530 for kekilla, and 600 for tea. The greatest number of species was represented in the pine seed bank with 26 out of the 46 documented species, followed by tea (15), forest (14), and then kekilla land (11).

Trees and shrubs (woody plants) represented approximately 31% of the germinating seed bank, all from soils of the forest, pine, and kekilla land. Melastomataceae shrubs comprised two-thirds of the germinant woody plant seed bank. One of the melastomes, *Clidemia hirta*, is an exotic invasive that we

found predominantly restricted to the soil seed bank of the forest. Germinants of tree species, mostly *Alstonia macrophylla* and *Trema orientalis*, were restricted to the pine and forest soils. All the recorded tree and shrub species are considered pioneers (Table S1). Herbs made up 50% of the total germinants in the soil seed bank across all land uses. The greatest density and number of species of germinants of herbs were found in the pine and tea land, mostly dominated by four species in the Rubiaceae (*Mitracarpus hirtus*, *Exallage auricularia*) and Scrophulariaceae (*Lindernia crustacea*, *L. pusilla*). Grasses made up 18% of all germinants, and the greatest numbers of species were found in the pine plantations; again most individuals were represented by soil seed banks in pine and tea lands, largely comprising two native species (*Cynodon arcuatus*, *Fimbristylis monticola*). Vines were found in low densities and were mostly restricted to the forest and pine soil seed banks (Table S1).

Germinant Richness, Density, and Diversity

Germinants from the soil seed bank all varied in species richness ($p < 0.019$), density ($p < 0.003$) and Shannon diversity ($p < 0.023$) across the different land use types (for statistical details see Table S2). The soils of the rainforest had the lowest species richness, density, and Shannon diversity as compared to the other land uses (Fig. 2). The other land uses had no differences among each other, while germinant density in pine plantations was as low as germinant density in forest (Fig. 2).

The Presence and Abundance of Soil Seed Bank Germinants in Relation to Land Use

Using the Jaccard distance measure, the effect of land use on species composition was significant ($p = 0.0001$). All land use types were significantly different from each other. The variance in the germinant species' community composition explained by land use was high (62.8%). The first ordination axis explained 42.9% of the constrained variation while the second explained 30.1% of the constrained variation (see Fig. 3). The soil seed bank of rainforest was largely defined by the presence of two native pioneer trees (*T. orientalis* and *Vitex altissima*) and the exotic invasive shrub *C. hirta*. Pine plantation was defined primarily by the presence of the herbs *Dorstenia indica* and *Exacum trinerve*, the grass *Fimbristylis nigrobrunnea*, and to a lesser extent the wind-dispersed tree *A. macrophylla* (Fig. 3). The soil seed bank of tea land was characterized by the presence of the herbs *L. crustacea*, *L. pusilla*, *M. hirtus*, and *Desmodium heterophyllum*, and the grasses *C. arcuatus* and *Cirtococcum* spp. Finally, the soil seed bank of kekilla land was characterized by the presence of three herbs (*E. auricularia*, *Spermacoce assurgens*, and *Vernonia cinerea*) and the grass *Scleria lithosperma*.

The effect of land use on species composition of the soil seed bank was also significant ($p = 0.00008$) using the Bray–Curtis distance measure, which emphasizes species' abundances, and all land use types were significantly different from each other. The variance in the germinant species' community composition explained by land use was high (72.0%). The first ordination
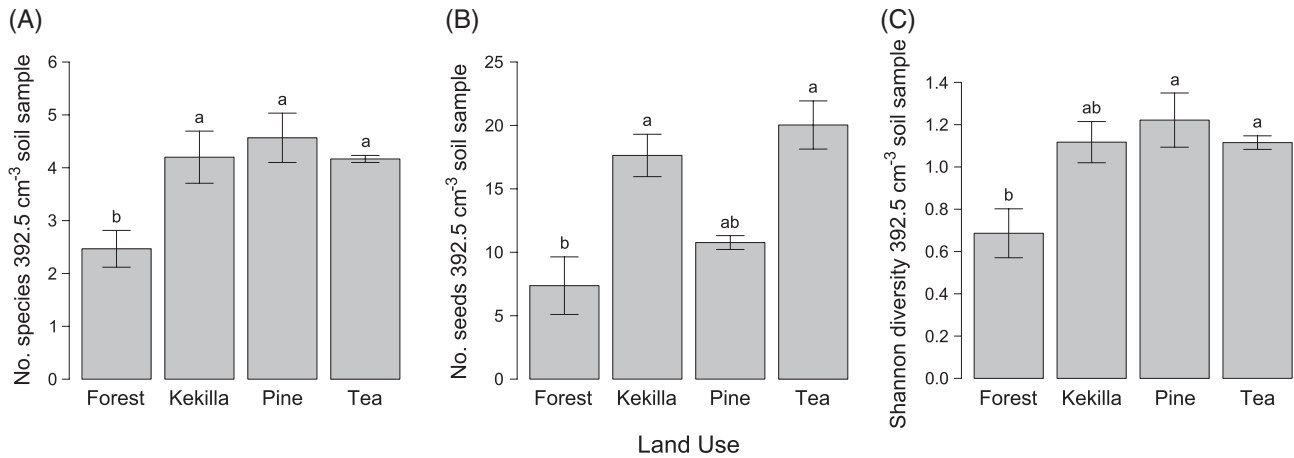
Figure 2. Comparisons of germinant: (A) number of species, (B) number of seeds, and (C) Shannon diversity indices across the different land use types. Error bars denote ± 1 SE. Tukey's test of multiple comparisons of means denote differences among land uses for the different measures ($p < 0.05$) except for comparisons for Shannon diversity ($p < 0.06$). Letters shared by the same land use are not significantly different (a > b).
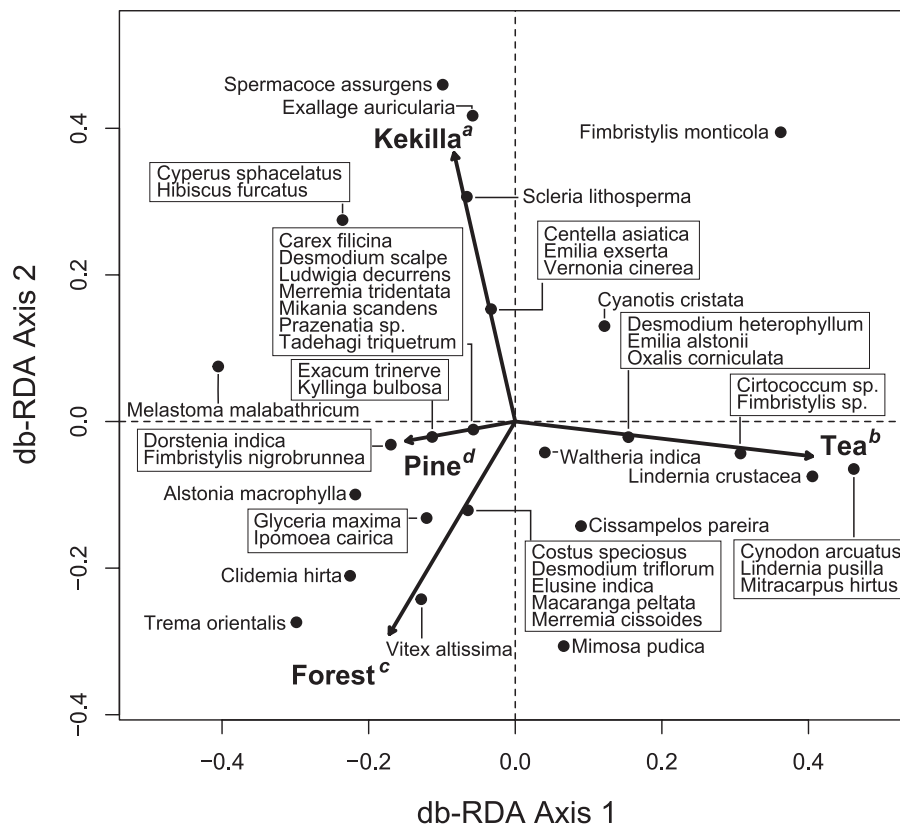

Figure 3. Distance-based redundancy analysis (db-RDA) ordination biplot (scaling 2) using the Jaccard distance matrix, which illustrates the presence/absence of species in the soil seed bank in relation to land use type. Similar superscripts (a > b > c) for the factor levels indicate no significant difference ($p < 0.1$) in species composition. All factor levels (land use type) were found to be significantly different from each other.

axis explained 47.1% of the constrained variation and the second axis explained 33.0% of the constrained variation (Fig. 4). Many species were not abundant enough to be well explained by the ordination but others were, indicating their dominance of the community. Soil seed banks of the rainforest had an abundance

of primarily two pioneer woody plants: *C. hirta* and *A. macrophylla*. Seed bank abundance of pine plantations was dominated by the pioneer tree *T. orientalis*. The kekilla land soil seed bank was defined primarily by the abundance of the woody pioneer shrub *Melastoma malabathrium* and the grass *F. monticola*. Tea
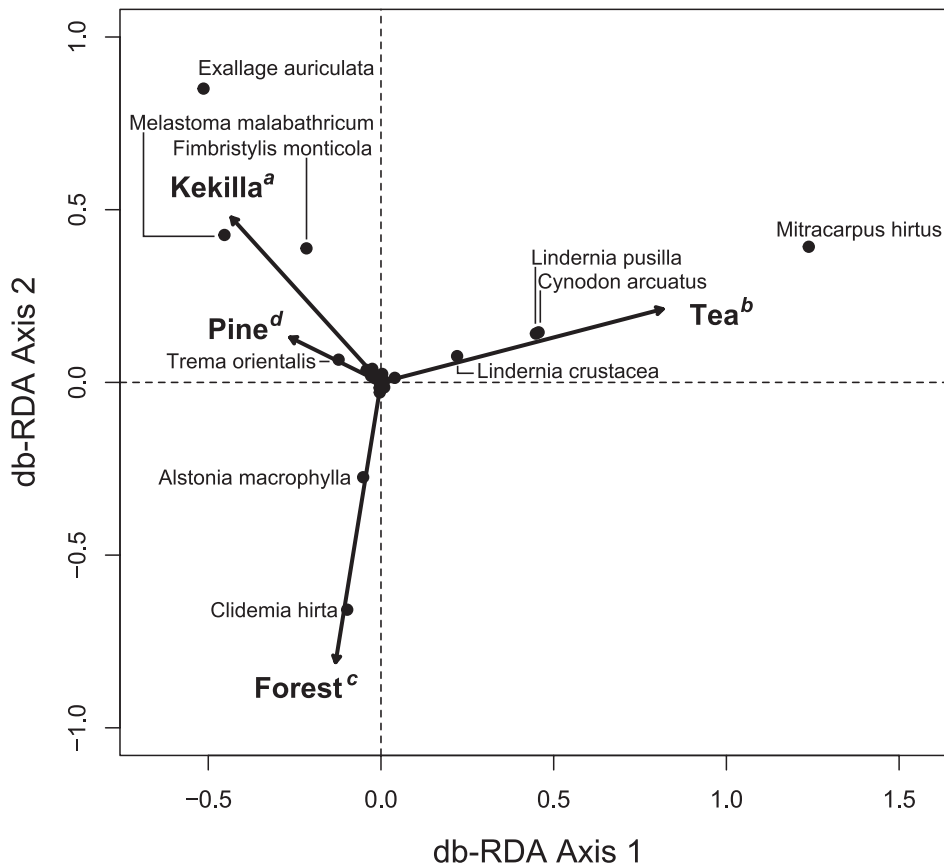
Figure 4. Distance-based redundancy analysis (db-RDA) ordination biplot (scaling 2) using the Bray–Curtis distance matrix, which illustrates the abundance of species in the soil seed bank in relation to land use type. Similar superscripts ($a > b > c$) for the factor levels indicate no significant difference ($p < 0.1$) in species composition. All factor levels (land use type) were found to be significantly different from each other.

land was characterized by an abundance of early-successional weedy herbs, including *L. crustacea*, *L. pusilla*, and *M. hirtus*.

Fourth-corner correlation analysis found that tree species were strongly positively associated with the soil seed banks of forests ($p = 0.038$), while herb and grass species were negatively associated with forests ($p = 0.038, 0.044$, respectively). The only other strong correlation we found was a negative association of shrub species with the soil seed banks of tea lands ($p = 0.038$) (Table 2).

Discussion

Many studies of tropical rain forests report that viable pioneer tree seeds stored in the soil can play a major role after natural or anthropogenic disturbances (Zimmerman et al. 2000), while the lack of pioneer tree seeds in the soil seed bank retards secondary succession (Wijdeven & Kuzee 2000). Viable seed storage of pioneer tree species in the soil seed bank serves as a key indicator for the assessment of the restoration potential of vegetation (Chen et al. 2013). The ex-situ transplant of the soil seed bank that contains seeds of many pioneer trees is one of the low-cost techniques that is recommended for restoration of

Table 2. Plant growth habit related to land use type. Fourth-corner correlation statistics $r(i,j)$ and probabilities (p) tested using 9,999 permutations followed by adjustment for multiple comparisons using false discovery rate (FDR) procedure. The global test of significance ($G = 7.036184$) and associated probability ($p = 1e-04***$) indicate a highly significant relationship between plant growth habit and land use type. Bold signifies a significant positive or negative relationship ($p < 0.05$) between specific land use types and plant growth habits. ***denotes significant at $p < 0.001$.

	Grass	*Herb*	*Shrub*	*Tree*	*Vine*
Forest					
$r(i,j)$	−2.604	−3.106	2.434	3.131	0.828
p	**0.044**	**0.038**	0.078	**0.038**	0.804
Kekilla					
$r(i,j)$	−0.244	−0.091	0.682	−1.543	−1.667
p	0.906	1	0.804	0.3024	0.328
Pine					
$r(i,j)$	1.642	1.432	−0.228	0.783	1.703
p	0.303	0.328	1	0.614	0.257
Tea					
$r(i,j)$	1.205	1.783	−2.837	−2.328	−0.852
p	0.367	0.247	**0.038**	0.078	0.614

vegetation on lands degraded by human activities (Parrotta & Knowles 2001).

Our results provide critical baseline data for the potential to understand under what circumstances, if desired, passive reforestation can be undertaken for rain forests in Sri Lanka, and more broadly for wet evergreen forests in South Asia (Western Ghats, India). Clearly, when Sri Lankan rain forests are cleared completely, which includes removal of all advance regeneration and destruction of the roots of the original forest, our study demonstrates the soil does not have the potential seed source for renewal and regrowth, which is necessary for regenerating a new forest. Our study showed that the soils of the rainforest have the lowest species richness, density, and diversity as compared to the other land uses. Only 59 tree seedling germinants were recorded, which belong to four different early-successional pioneers; overwhelmingly dominated by the non-native tree *Alstonia macrophylla*. This comprises about 250 viable seeds/m^2 of which 88% are exotic; only 22 viable seeds/m^2 comprise native pioneer trees. In comparison, Australian rain forests studied by Graham and Hopkins (1990) recorded 204 seeds/m^2; while in another study Hopkins et al. (1990) estimated the viable soil seed bank to be 400–600 seeds/m^2. Both studies indicate that the majority of species are native pioneer trees and shrubs and none were indicated to be exotics. Similarly for a Panamanian forest, Dalling et al. (1997) recorded mostly germinants of pioneer trees that were between 330 and 1,090 seeds/m^2 depending upon dry and wet season, respectively. And in the Atlantic wet forests of Brazil, mature rainforests comprised between 389 and 482 viable seeds/m^2 (Baider et al. 2001). All these studies from wet evergreen rain forests show there is little to no association between the composition of the rain forest vegetation and the seed bank, or between the annual seed rain and the seed bank (Hopkins & Graham 1983; Dalling et al. 1998; Mall & Singh 2014). Our study was no exception, as we found no late-successional tree species represented in the seed bank as defined by floristic studies of the rainforest conducted by Gunatilleke (2004).

Vines represented a very low density and are mostly restricted to the forest and pine soil seed banks. This is contrary to findings in other forest types and especially disturbed forests of Australia (Hopkins & Graham 1983; Graham & Hopkins 1990) and Central America (Young et al. 1987; Dupuy & Chazdon 1998). However, other studies support our findings where overall densities of vines are low in both pastures and forest; but vine densities were still higher in the forest soil as compared to pastures (Wijdeven & Kuzee 2000). The presence of vines in soil seed banks can inhibit regrowth because of their fast growth and ability to smother competition. The near absence of vines in the soil seed bank of our study suggests that they may play a less significant role in inhibiting spontaneous reforestation processes of disturbed and cleared lands for this region.

Interestingly pine plantations show almost an equal number of tree seedlings germinating as the rainforest, but species composition was different, with pine plantations primarily comprised of the native pioneer *Trema orientalis* instead of the exotic *A. macrophylla*. Similarly, the native Melastomataceae shrub species (*Melastoma malabathricum*) predominated

beneath the pine rather than the exotic (*Clidemia hirta*), which was the major shrub represented in the soil seed bank of the rainforest. Seed bank germinant densities in the pine plantations had equally low densities as the rainforest but significantly higher Shannon diversity. The higher diversity and the fact that, of the three altered land uses, pine was the only one that comprised tree germinants in any numbers makes it the one land use that might be restored to a very simplified second-growth without any planting. The change in seed bank composition between kekilla fern land and pine might be related to the time elapsed as the pine was planted on fern land, with the cover of the young pine forest enabling the soil seed bank to build up both in diversity of growth habits and species, especially in pioneer tree species. This is corroborated by others that report sites surrounded by disturbed areas such as plantations and pastures had high soil seed storage densities and contained large numbers of seeds of light-demanding shrubs, and herbaceous and graminoid species because the seed inputs of pioneer species from arboreal birds and mammal are perhaps drawn to the cover and structure of the pine (Quintana-Ascencio et al. 1996; Parrotta & Knowles 2001; Chen et al. 2013).

There are several studies that suggest shrub species that originated from the buried seed bank can grow, then shade the competition, and then facilitate the dispersal and establishment of animal-dispersed trees as well. For example, shrubs can be a "successional facilitator" within pastures of the Amazon (Vieira et al. 1994) and Costa Rica (Holl 2002). Shrubs that can establish in open areas and that originate from the seed bank (such as the melastomes in our study—both bird dispersed) can potentially facilitate early secondary succession following the nucleation model (Yarranton & Morrison 1974). These species attract birds, small mammals, and bats and in so doing promote native rainforest regeneration under their canopy.

Tea was the one land use with the greatest density of germinants within the soil seed bank with over double the number as compared to pine and the rainforest. However, none were woody trees and shrubs. Seeds of herbaceous and graminoid species dominated the soil seed banks of the tea lands. Not surprisingly, several are exotic and invasive species (e.g. *Mitracarpus hirtus*, *Lindernia crustacea*); many of the herbs recorded, in general, have known Ayurvedic medicinal value. Given this floristic trend, tea lands have the lowest restoration potential of the three altered land uses. Because of continuous cropping and weeding it is not a surprise that the seed bank comprises mostly short-lived annual and perennial weedy herbs and grasses. This species composition of the soil seed bank of tea lands likely make these lands unsuitable for facilitating forest restoration because of potentially high grass and herb competition with either planted tree seedlings or natural forest regeneration resulting from wind- or animal-dispersed seeds (Hooper et al. 2002). However, there are several nitrogen-fixing herbaceous ground covers in the Fabaceae (*Desmodim* spp., *Mimosa pudica*) associated mostly with tea land and pine plantations that may have potential as a live mulch and organic fertilizer and that could aid the establishment of planted tree seedlings for reforestation.

Our results are somewhat contrary to studies in the Neotropics on old fields and second-growth forest. In the

Neotropics disturbed landscapes comprise seed banks with early-successional herbs, trees, and shrubs that have a greater capacity to contribute to the passive reforestation of old pastures and agricultural fields than our study shows for the Sri Lankan rainforest region. Studies in Costa Rica (Butler & Chazdon 1998) and the Atlantic rainforest region of Brazil (Rico-Gray & García-Franco 1992) report much higher numbers of pioneer trees and shrubs in soil seed banks compared to our study, necessary for jump-starting successional processes that can revert vegetation back to forest.

In summary, soil seed banks comprised twice the densities of seedling germinants in tea and kekilla fern lands as compared to pine and forest. However, the seed banks in tea and kekilla fern land were absent of any tree seed. They largely comprise well known weedy herbs and grasses. This is one explanation as to why agricultural lands such as tea do not revert back to forest easily in this region but are quickly colonized by ferns and grasses such as kekilla. Under these circumstances, choices for restoration back to native forest are restricted to planting. This contradicts studies of pasture and agricultural fields in the Neotropics where soil seed banks are potential sources for propagating second-growth natural forest. In our study, pine plantations are the one land use that may facilitate some tree and shrub regeneration through the seed bank. Interestingly, for unknown reasons, the two major invasive exotics (*A. macrophylla* and *Clidemia hirta*) appear largely restricted to the soil seed banks of the mature rainforest. More studies are needed to understand why this is so.

Acknowledgments

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Number of germinants recorded within the soil seed bank by species and land use type, organized by growth habit.

Table S2. One-way nested ANOVA (sample nested within site), testing the effect of land use type on three response variables.