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Natural or assisted succession as approach of forest recovery on abandoned lands with different land use history in the Andes of Southern Ecuador

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Abstract Forest recovery on disturbed areas is of special significance in the Ecuadorian Andes, where deforestation is a serious problem. Natural diachronic succession was evaluated on three large plots or sites, differing in their land use and vegetation composition, one is dominated by grass species on an abandoned pasture (Pasture site), the other two are post-fire vegetation dominated by bracken (Bracken site) and various shrubs (Shrub site). Additionally, we assessed the effectiveness of manual removal of competitive herbaceous species to accelerate forest recovery. Monitoring was done in 2003, 2005 and 2007 on 48 subplots of 116 m^2 each recording species richness and woody-species density. Results showed that the Pasture site demonstrated a competitive effect of exotic grasses on woody species recruitment with much lower species recruitment and density, suggesting serious inhibition of natural forest regeneration and an unclear successional trajectory. The Bracken and Shrub sites became significantly similar floristically and there is evidence for a marked facilitation of woody plant recruitment correlated with light availability on the ground. Both sites showed characteristics of classic succession, with Shrub showing a higher species richness and density while late-successional species are poorly represented on the Bracken site. However, NMDS ordination using species density showed that the two trajectories may not be converging towards a common "final state". Manual weeding was ineffective for accelerating forest recovery. These results suggest that the main limiting factor for the recruitment of woody species on the Pasture site is strong grass competition and must be addressed before seed availability, while seed availability seems to be the

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constraining factor for Bracken and Shrub site development, thus direct seeding or planting may be effective in accelerating forest recovery.

Keywords Andes region · Abandoned lands · Restoration · Mechanical treatment · Successional trajectory

Introduction

Natural succession has been shown to be a valid approach to restore woodlands with advantages such as low costs (Hooper et al. 2005; Sampaio et al. 2007) and a relatively high floristic diversity when compared to other methods such as tree planting (Engel and Parrotta 2001), where a limited number of tree species may be used. The recovery process depends on several factors such as land-use history (Aide et al. 1995; Chinea 2002; Klanderud et al. 2010), land-use intensity (Guariguata and Ostertag 2001), seed availability (Wijdeven and Kuzee 2000), grass competition (Holl et al. 2000), time since abandonment (Pascarella et al. 2000) and distance from existing forests (Hooper et al. 2005; Günter et al. 2007). This study focuses on the effects of natural and assisted succession on forest recovery on three abandoned areas with different land use history and vegetation composition.

In the context of forest recovery, interspecific interactions such as competition and facilitation play an important role in community dynamics (Ding et al. 2016) and interactions between biotic and abiotic factors also affect the rate and direction of successional trajectories (Holl et al. 2000). Several studies in the tropics suggest that exotic grasses can impede tree establishment (Holl 1998a; Rhoades et al. 1998; Hooper et al. 2005; Sampaio et al. 2007) due to competition for light, nutrients and water.

Some studies have shown bracken fern, *Pteridium* spp., to be a competitive species that negatively affects the natural succession process (Marrs et al. 2000; Beck et al. 2008a). Also several studies have indicated that shrubs facilitate tree seedling establishment (Vieira et al. 1994; Holl 2002) and aid rapid accumulation of new species (Capers et al. 2005) in abandoned tropical pastures. Among the reasons postulated are the presence of arbuscular mycorrhizal associations (Muthukumar et al. 2003) as well as better nutrient cycling and soil conditions (McDonald and Healey 2000).

These ecological aspects in the context of forest recovery have high relevance especially when vast areas have been degraded and biological species richness is implicitly at risk. A clear example of this is Ecuador, which is recognized as one of the megadiverse countries in the world, where the forest loss between 2000 and 2008 was 19,000 km^2 (Sierra 2013). The Andes region has been subject to human-induced forest clearance for the last 10,000 years for agricultural purposes (Pearsall 1992), and land reforms in 1964 and 1973 encouraged the colonization of new areas, which has led to the intensification of land-use transformation in the last few decades (De Zaldívar 2008).

Our study area, the San Francisco Valley in Southern Ecuador, was opened up to rapid colonization in the 1960's by the completion of the road between Loja and Zamora (Niemann and Behling 2008), and since then has been subject to the conversion of old growth forest to pasture, mainly for cattle grazing. The usual technique for forest clearance employed in this area is slash and burn (Beck et al. 2008a) which implies clearing the natural forest and burning regularly for weed control and pasture rejuvenation (Knoke et al.

2014). Furthermore, the fires set by farmers to create grassland are frequently uncontrolled and may burn a whole mountainside. In the long run, these fires are detrimental to grazing as they encourage fire-tolerant species such as bracken fern while weakening the competitive strength of native grass species (Beck et al. 2008a; Roos et al. 2011). When these converted lands become unproductive they are abandoned (Weber et al. 2008), which has significant implications for farmers who will either suffer a reduction in income or convert new areas of forests.

Forest recovery on abandoned or degraded land can be encouraged by silvicultural measures such as removing grass competition (Williams-Linera et al. 2016), tree planting (Sampaio et al. 2007), direct seeding (Engel and Parrotta 2001; Doust et al. 2008) or providing perch trees (Holl 1998b). Although there is a lack of experimental evidence of multiple stable states (Newton and Cantarello 2015), a growing body of literature suggests that some ecosystems may have alternative stable states and alternative successional trajectories (Suding et al. 2004; Schröder et al. 2005). If hysteresis is suspected in a site, then assisted succession may be required to shift from one stable state to another. In this study three large plots with differing past land uses were evaluated for diachronic succession; one is dominated by an exotic grass species on an abandoned pasture (Pasture site), while the others are post-fire vegetation dominated by bracken (Bracken site) and shrubs (Shrub site); all sites were abandoned at different times, leaving the possibility that these sites show synchronic succession. Since local farmers usually apply manual weeding methods, mainly using machetes in order to maintain the pastures, we also ask if removal of competitive herbaceous vegetation on Bracken and Shrub sites could support forest recovery.

The purpose of this study was to understand the vegetation dynamics on these three distinct sites in order to improve restoration techniques in a tropical mountain forest ecosystem. The specific objectives of this study were to (1) identify effects of time since abandonment on species richness and density and detect possible triggers for woody species recruitment of sites with different vegetation cover; (2) evaluate if removal of competing herbaceous ground vegetation can accelerate forest recovery; and (3) evaluate the successional pathways of the sites through vegetation dynamics. The results may influence silvicultural rehabilitation efforts in the tropical mountain forest region of Southern Ecuador indicating site-specific management recommendations.

Methods

Study site

The study area was adjacent to the Reserva Biológica San Francisco (RBSF) (Lat 3°58′30″S, Long 79°4′25″W), 34 km southeast of Loja, Ecuador. Pasture, Bracken and Shrub sites were located on south-facing slopes heavily affected by human activity, and all sites were similarly isolated from the adjacent old growth “tropical mountain rain forest” (Beck et al. 2008b), on the other side of the valley by the San Francisco River and the Loja-Zamora road. Mean annual rainfall is 2000 mm at 1800 m asl with an extremely wet season from April to July and a less humid period from September to December. The mean annual temperature is 15.3 °C (Bendix et al. 2006).

Three four-hectare plots were established in 2002 according to their vegetation type (pasture, bracken and shrub) for this long-term monitoring project. The distance between sites was approximately 3 km. All three sites had a combination of soil types corresponding mostly to cambisols, planosols, histosols, umbrisols and podzols (Wilcke et al. 2008). The comparability of the study sites regarding soil conditions has been shown in Günter et al. (2009). The land-use history was determined by means of aerial photographs (1962, 1976, 1989 and 1998) and confirmed by interviews with neighboring landowners. Thus, the three sites are comparable with respect to soils, climate, exposure and slope, and represent approximately 48% of the land use in the San Francisco valley with the rest comprised of native forest and various other different uses (Göttlicher et al. 2009). The difference between the areas is thus land use history, resulting in different vegetation cover. Moreover, each site was embedded in a matrix of like vegetation to minimize edge effects (i.e. the Pasture site was surrounded by pasture cultivated with *Setaria sphacelata*).

Sites descriptions

Pasture site (elevation 1800–2100 m asl)

The area is dominated by *Setaria sphacelata*, an introduced species from tropical Africa which can reach an average height of ~70 cm in only 18 months (Roos et al. 2011). This species was cultivated since the initial slash and burn forest clearance (pers. comm. with locals). Other, less dominant grasses include *Melinis minutiflora* P. Beauv, and sparse patches of bracken fern (*Pteridium arachnoideum* (KAULF.) MAXON) can also be found. According to aerial photography, the natural forest was cleared over 36 years ago. The slope ranges from 15° and 38°. Before the experiment started in 2003, the site was actively used for cattle grazing. At the beginning of the experiment, the site was fenced off to prevent cattle invasion.

Bracken site (elevation 1900–2100 m asl)

This site is covered with bracken fern (*Pteridium arachnoideum),* which is well known as a fire-tolerant species. Aerial photography reveals that the forest was originally cleared over 23 years ago and since then the whole site has been burnt at least 4 times but never cultivated with *S. sphacelata* and the last fire event was approximately 12 years ago (pers. comm. with locals). The slope ranges between 23° and 43°.

Shrub site (elevation 2100–2200 m asl)

This site, originally cleared over 50 years ago is considered secondary forest as it has been in unmodified natural succession for over 25 years since the last fire event. It is also the result of recurrent fires without *S. sphacelata* cultivation. Several woody species are present but the most abundant are *Ageratina dendroides* (Spreng.) R.M. King & H. Rob. and *Myrsine coriacea* (Sw.) R. Brown. The slope ranges between 5° and 43°.

In the two latter sites the reasons for initial and repeated burning are not well understood, but most likely occurred either by accident or to promote grazing.

Experimental design

In 2003, sixteen 10.8 × 10.8 m subsamples were established on each plot for the monitoring of natural and assisted succession. Half of the subsamples were randomly selected and manually treated by cutting back all competing herbaceous species with a machete every 4 months from 2003 to 2005. The total area sampled at each site was 1866 m^2. Competing species refers to dominant, exotic and aggressive species such as grasses (*S. sphacelata*) in the Pasture site, and exotic fern (*P. arachnoideum*) in the Bracken and Shrub sites, woody native species were not removed.

Data collection

In 2003, 2005 and 2007, hereafter referred to as "0 months", "24 months", and "48 months" respectively, all woody species were registered and identified in each plot. Species were categorized as shrub, treelet or tree, based on field observations and the Vascular Plants Catalogue of Ecuador (Jørgensen and León-Yánez 1999). In each subsample, the number of all individuals higher than 30 cm was counted and each plant received an identification tag and the following information was recorded: species, height (cm), root collar diameter (cm) and number of stems. The biotic factors Leaf Area Index (LAI) and Woody Volume Index (WVI) ($\pi \times 0.5 \times$ (basal diameter)^2/4 $\times$ height) (Wishnie et al. 2007) were measured on a subsample basis at 48 months. LAI (LAI 2000, Licor, Nebraska, USA) was measured at 30 cm at forty points regularly distributed in each subsample and then an average was calculated; measurements were recorded under cloudy conditions following the manufacturer's guidelines (LI-COR 1992). To avoid the excessive influence of slope, the data of rings 4 and 5 were excluded.

The neighboring pristine forest of the RBSF was chosen as the reference ecosystem as it has been intensively studied, resulting in available checklists of biological diversity for various different groups of organisms (Homeier and Werner 2007; Beck et al. 2008b). Comparison of the floristic composition between study plots and old growth forest was based on studies performed by research groups at the RBSF (e.g. Dislich et al. 2009).

Data analysis

We analyzed the effects of treatment and time on the richness and density of woody species using Generalized mixed-effects models (GLMM) with nested random factors and a Poisson error distribution model with log-link. The fixed effects were time and treatment and their interaction with nested random effects to take into account the lack of true replicates and the presence of repeated measures; thus subsamples were nested within sites with time as the repeated measures. All analyses included a null model and model fit was assessed using Chi square tests on the log-likelihood values to compare the full model to the null model and the models were tested for overdispersion. Analyses were performed with the R package "lme4" (Bates et al. 2015).

Individual-based rarefaction curves were computed to explore the relationship between species number and density and these were calculated across time for each successional site in Ecosim version 7.0 (Gotelli and Entsminger 2009). Evenness and Shannon indices were computed at the plot level in each study site according to time and the results were statistically tested using one-way ANOVA followed by a Tukey comparison test considering time as a factor; assumptions of normality and homogeneity of variance were achieved. Chao's Sørensen measure based on abundance was compared between each pair of sites (Pasture-Bracken, Bracken-Shrub, and Shrub-Pasture) over time to confirm similarity (Chao et al. 2006) using EstimateS 8.2.0. (Colwell 2009). A Mantel Test implemented using Monte Carlo Permutation was used in order to explain the relationship between floristic composition and site at 48 months.

Generalized linear Mixed Models using Penalized Quasi-Likelihood estimation (PQL) with nested random factors and a Poisson error distribution with log-link were used to quantify the effects of LAI and WVI on species richness and density at 48 months while taking into account random variation in our sites. The fixed effects were LAI and WVI and their interaction with nested random effects, subsamples nested within treatments within sites. PQL was chosen to take into account overdispersion detected in GLMM with Laplace approximation. This analysis was performed using the function ‘glmmPQL’ in the R package ‘MASS’ (Venables and Ripley 2002).

Furthermore, non-metric multidimensional scaling (NMS) based on species richness and density at 0 and 48 months was conducted using the Sørensen Distance (Bray–Curtis Distance) in order to determine the successional pathways of the three sites. An autopilot mode was chosen for constructing multiple runs, finding the best solution for each dimensionality and for testing statistical significance.

Indicator Species Analysis was used to analyze species change on each site at the beginning and end of monitoring in order to better understand the evolution of some of the ecological processes over time. Indicator values were calculated according to Dufrene and Legendre (1997) (see also McCune and Grace 2002). Two groups (0 and 48 months) were formed and the indicator values were tested for statistical significance using a Monte Carlo technique. These analyses as well as the Mantel Test were performed in PC-ORD 5.14.

Results

Influence of time and treatment on the recruitment of species richness and density

The results from the GLMM showed, as expected, time generally had a high statistical significance for species richness and density over time (both variables; $p < 0.001$) (Table 1). This means that all sites showed an increment for both variables across time, with the Bracken and Shrub sites being the most dynamic (Fig. 1b, c); in contrast, the Pasture site had a slight increment in species richness in the first observation period but reduced density in the second observation period (Figs. 1a, 3b). A statistical significance

Table 1 Influence of time (0, 24 and 48 months) and treatment (clearing of competing herbaceous species) and its interaction on species richness and density of seedlings according to Generalized linear mixed model (GLMM), three periods of monitoring at 0, 24 and 48 months, n = 24

Fixed effects	Estimate	SE	Z value	*p* (<0.05)
Species richness				
Time	0.231	0.054	4.296	<0.001***
Treatment	−0.212	0.156	−1.358	0.174
Time × treatment	0.086	0.040	2.122	0.034*
Density				
Time	0.339	0.068	4.991	<0.001***
Treatment	−0.129	0.259	−0.496	0.620
Time × treatment	0.040	0.042	0.965	0.335

* p < 0.05

*** p < 0.001

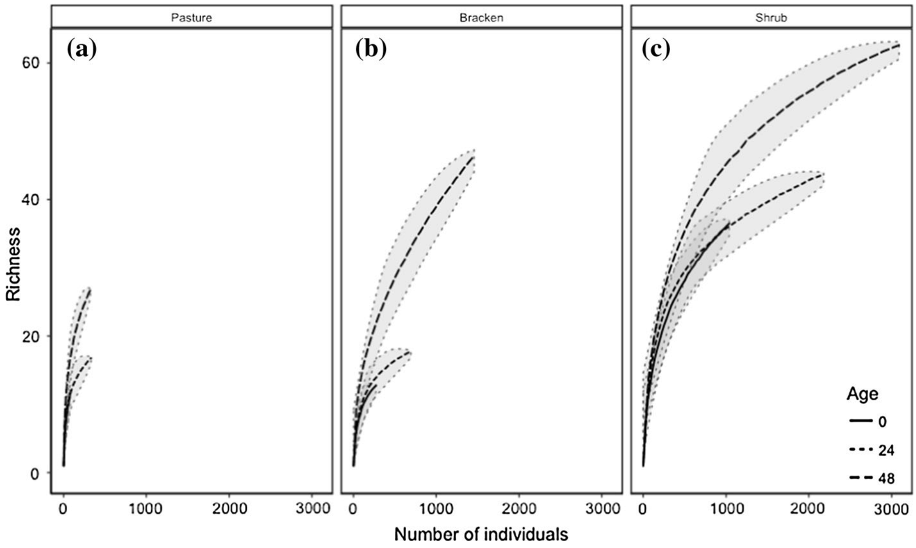

Fig. 1 Individual-based rarefaction *curves* per site over time for manual weeding and untreated *plots* combined: Pasture site (**a**), Bracken site (**b**) and Shrub site (**c**). Sampling area per site is 1866 m^2. *Shadowed areas* show the 95% confidence intervals

was found for the interaction between time and treatment ($p = 0.034$) on species richness, which indicates that the untreated treatment contributed to increasing the number of species over time mainly on Bracken and Shrub sites.

Bracken and Shrub sites showed marked increases for Shannon Index, with the Shrub site having the highest value (Table 2). The diversity on the Pasture site showed change in the second observation period but was not highly significant from the first observation, while the Bracken site was characterized by the highest dynamics. The Evenness values comparing Pasture with Bracken and Shrub sites confirmed these findings. The Shannon Evenness (Table 2) and Chao's Sørensen Index (Table 3) indicated that the Bracken site had a higher similarity to the Shrub site throughout the study. There was also a high correlation ($r = 0.64$, $p = 0.001$) among sites and community similarity according to the Mantel Test.

Potential drivers for diversity of woody plants

The only statistically significant factor that influenced the recruitment of woody species at 48 months was LAI for both species richness ($p = 0.004$) and density ($p < 0.001$), suggesting that recruitment of new species and individuals depended on the availability of light, with higher light intensities being favorable for species richness and density (Fig. 2a–c). A gradient of light from Pasture followed by Bracken and Shrub was found on LAI basis, where Pasture had the highest shade due to dense cover of *S. sphacelata*. Woody Volume Index (Fig. 2b), and the interaction between WVI and LAI did not show any significant effect on species richness although it was observed that the highest LAI corresponded to the lowest WVI (Fig. 2a, b). On the other hand, WVI ($p = 0.082$) had no influence on density although with higher WVI a higher density was observed (Fig. 2d); the interaction LAI with WVI ($p = 0.154$) also had no significant effects on density.

Table 2 Mean (±SE) Shannon (H′) and Evenness (E′) indexes per site (Pasture, Bracken and Shrub)

Site	0 months		24 months		48 months	
	H′	E′	H′	E′	H′	E′
Pasture	0.19_{a} (±0.21)	0.18_{a} (±0.19)	1.03_{ab} (±0.55)	0.71_{a} (±0.31)	1.06_{b} (±0.64)	0.63_{a} (±0.33)
Bracken	0.25_{a} (±0.21)	0.18_{a} (±0.14)	0.81_{a} (±0.40)	0.51_{ab} (±0.24)	1.63_{b} (±0.37)	0.68_{b} (±0.13)
Shrub	0.57_{a} (±0.09)	0.27_{a} (±0.04)	1.67_{b} (±0.29)	0.66_{a} (±0.10)	1.83_{b} (±0.19)	0.66_{a} (±0.06)

Different letters correspond to significant differences ($p < 0.05$) according to Tukey HSD comparison between times within the site

Table 3 Comparison of floristic composition among sites at 0, 24 and 48 months of observation period according to Chao Sørensen Est–density per successional site (±SD) (n = 24)

Site	0 months	24 months	48 months
Pasture versus Bracken	0.29 ± 0.37	0.54 ± 0.34	0.38 ± 0.31
Pasture versus Shrub	0.32 ± 0.39	0.55 ± 0.31	0.41 ± 0.34
Bracken versus Shrub	0.63 ± 0.29	0.71 ± 0.23	0.70 ± 0.19

A higher value indicates higher similarity in the floristic composition of sites

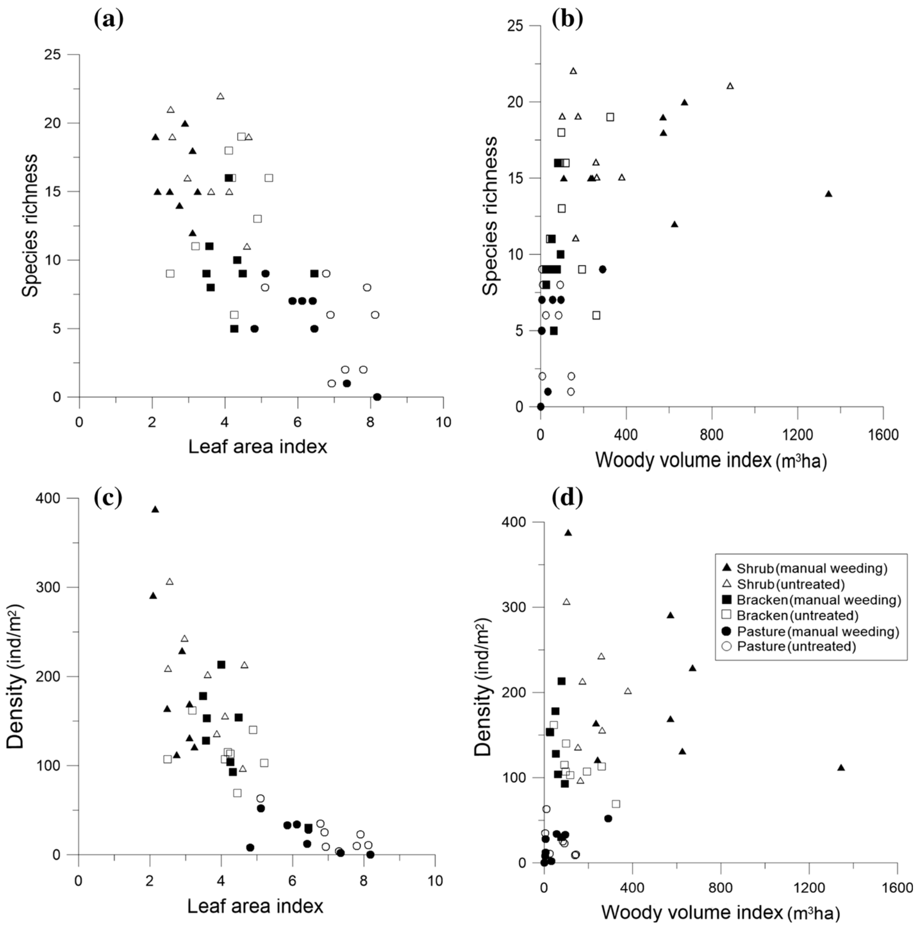

Fig. 2 Relationship between species richness and density with Leaf area index (**a**, **c**), Woody volume index (**b**, **d**), Pasture site (*circles*), Bracken site (*square*) and Shrub site (*triangles*). *Filled shapes* denote manual weeding *subplots* and *open shapes* denote untreated *subplots*. Sampling area per site is 1866 m^2

Effect of manual weeding on species richness and density across time

Treatment alone used in GLMM had no significant effect on species richness and density; therefore the manual treatment did not contribute to increasing woody diversity (Fig. 3a–

f). A greater increase of species richness on the Bracken and Shrub sites mainly at 48 months was found on untreated subplots, therefore suggesting an actual negative effect of manual treatment on species recruitment or survival (Fig. 3c–e). There was a significant result for the interaction between treatment and time for richness ($p = 0.034$), this means that species richness increases over time in general with a greater increment on untreated subplots (Fig. 3a, c, e). The effect of treatment ($p = 0.335$) and its interaction with time on density showed no differences (Fig. 3b, d, f).

Ordination of the three sites at 0 and 48 months

In total 1463 individual plants of 43 species and the 5386 individual plants of 92 species present at 0 and 48 months respectively were ordered by non-metric multidimensional scaling (NMS). The first three axes explained 71.9% of the variation. Figure 4 shows that Bracken and Shrub sites followed an almost parallel, or a slightly convergent successional pathway, while at the Pasture site the floristic composition of each subplot was widely dispersed and showed no clear pattern of successional trajectory.

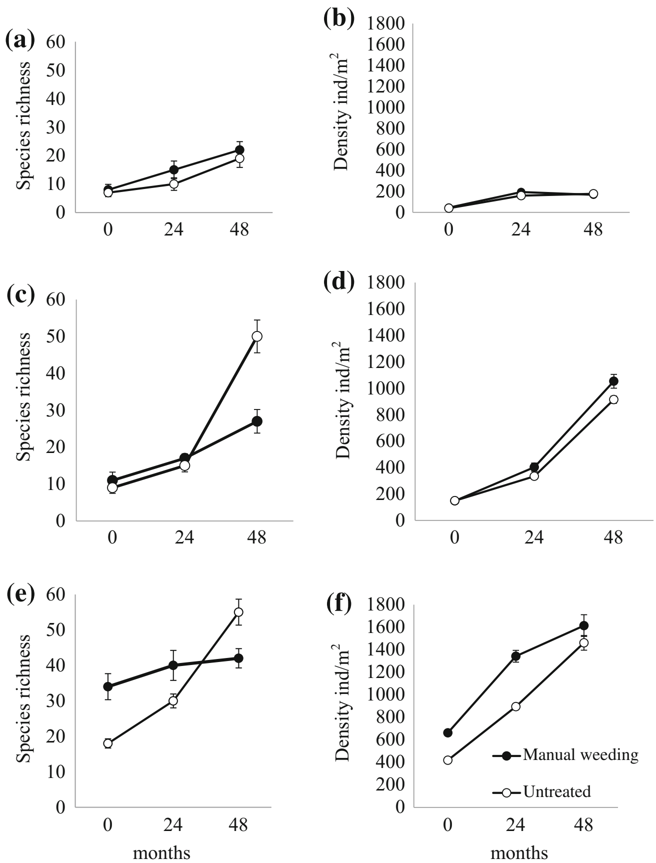

Fig. 3 Effects of mechanical treatment (clearing of competing herbaceous species) on species richness and density at 0, 24 and 48 months per site: pastures (**a**, **b**); bracken (**c**, **d**) and shrub (**e**, **f**). *Open circles* correspond to Unteated and *full circles* correspond to Manual weeding. *Bars* represent standard deviation. Sampling area per site is 1866 m^2. Data are averaged by treatment

Indicator species analysis

The Pasture site maintained the same indicator species (*Baccharis latifolia*) during the two observation periods but a new species (*Ageratina* sp.) became significant by the end of the monitoring (Table 5). On the Bracken site the floristic composition clearly shifted since more species became significant by the end of monitoring (*Baccharis brachylaenoides, Baccharis* sp., *Baccharis tricuneata*, *Vernonia* sp., *Escallonia paniculata*, *Monochaetum lineatum, Roupala montana*). It is notable that all of them have wind-dispersed seeds. On both sites a high dominance of pioneer species and shrub life–forms was evident (Tables 4, 5). In the Shrub site new species joined the list of indicator species with the highest significance at 48 months (*Ilex* sp., *Baccharis macrantha*, *Baccharis* sp., *Viburnum pichinchensis*, *Clethra fagifolia*, *Clusia* spp., *Macleania poortmani*, *Vaccinium floribundum*, *Alchornea pearcei*, *Macrocarpaea* sp., *Persea* sp., *Palicourea* sp., *Hesperomeles obtusifolia*, *Palicourea anceps*) and in contrast to the other two sites, most species exhibited seed dispersal by animal vectors (Tables 4, 5). The dominating life–forms are treelets and trees, probably recruited from seed dispersed by birds or bats.

We compared the floristic composition at our sites with the adjacent old growth forest in terms of presence (P) or absence (A). The results revealed that of the 32 woody species with highest statistical significance in our sites, only 13 were registered in the adjacent reference forest. The majority of these species were found on the Shrub site (Table 5).

Discussion

Land use history and time influencing the natural succession process

In our study area, at the beginning of the monitoring, the effect of former land uses and time since abandonment was clearly visible in the field: the Pasture site showed a considerably lower woody species diversity in comparison to the Bracken and Shrub sites. Later, on the Shrub site there was an increase in woody species diversity during the

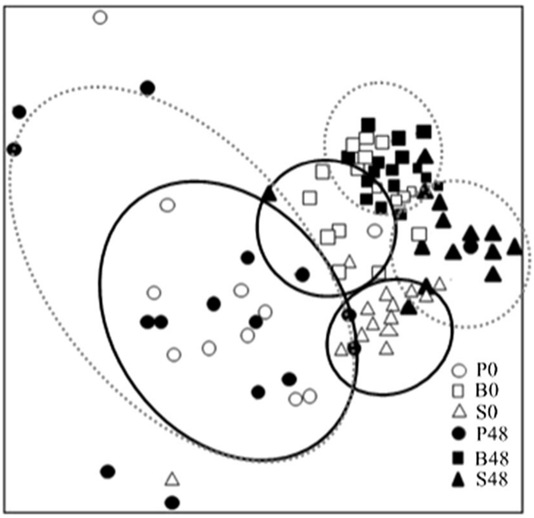

Fig. 4 Non-metric multidimensional scaling ordination based on species richness and density of woody regeneration on three sites: *P* pasture, *B* bracken and *S* shrub, at 0 months (*open symbols*) and 48 months (*full symbols*). The *full circles* indicate the conditions at 0 months, the *dashed circles* those at 48 months. The Monte Carlo *p* value is 0.0040 and the final stress is 16.14

Table 4 Ecological characteristics of indicator species among sites ($p < 0.05$) and between the initial (0 months) and final observation period (48 months)

Ecological characteristics	Pasture		Bracken		Shrub	
	0 months	48 months	0 months	48 months	0 months	48 months
Total number of woody species	2	2	1	7	6	19
Assignment to dispersal mechanism (animal/wind)	0/2	0/2	0/1	0/7	3/3	12/7
Number of species in old growth forest (absent/present)	0/2	0/2	0/1	1/6	4/2	9/10
Affiliation of life form (treelet/tree/shrub)	0/0/2	0/0/2	0/0/1	1/1/5	3/1/2	5/8/6

Characteristics considered were: dispersal syndromes, presence in adjacent old growth forest and life form

monitoring period, but the rapid development on the Bracken site was especially surprising. Previous studies (e.g. Aide et al. 1995) demonstrated that abandoned tropical pastures show little progress during the first 10 years, and need a full fifteen years to show significant woody development, which is in line with our results. Other studies have shown similar trends (Pascarella et al. 2000; Chinea 2002), suggesting that the Bracken and Shrub sites may have passed a threshold and are now following relatively fast successional trajectories. The Shrub site especially has the advantage of existing woody vegetation, which provides seed availability and attracts seed dispersers, which favors dynamic woody species recruitment (Vieira et al. 1994).

Competition and facilitation: drivers for woody species diversity

Natural interactions in plant communities such as competition and facilitation are very complex and might enhance or delay the restoration processes by modifying environmental stress and resource availability (Callaway and Walker 1997). We assume that these two interactions are underlying reasons for the woody species recruitment results. While they were not the objective of our research hypothesis, they should be discussed in light of our results.

The competition by grasses is among the most important barriers for forest regeneration of former pastures (Aide et al. 1995; Holl 1998a; Ortega-Pieck et al. 2011). Therefore, the low species richness and density on the Pasture site with highest LAI and lowest volume index suggest very strong competition from the dominant grass species *S. sphacelata.* The dense vegetation on pasture sites represents a physical barrier for seedling establishment, and the excessive shading inhibits the development of seedlings. Additionally, former studies have shown an additional negative effect of root competition of grasses on initial plant performance due to high below ground biomass allocation in comparison with tree seedlings (Hooper et al. 2002). Likewise, net mineralization and nitrification in open pastures can be five times lower than under tree canopy (Rhoades et al. 1998) and prevent the establishment of other species. Given these competitive advantages, the dominance of *S. sphacelata* could likely form a more or less stable state—a degraded non-successional community with only a few species being able to establish themselves on the open area (Verdú et al. 2009). One practical solution to combat *S. sphacelata* competition is through planting light demanding tree species which shade the grass and consequently reduce or eliminate this strong competition (Celis and Jose 2011). Günter et al. (2009) recommend *Alnus acuminata* Kunth (aliso) as a suitable species in our case for this process, which could also act as a nurse species and facilitate further species recruitment. This is also in line with the establishment of woodland islets suggested by Rey Benayas et al. (2015), which were shown to accelerate restoration processes in Mediterranean agricultural landscapes.

On the other hand, the more complex vegetation on the Bracken and Shrub sites may already act as a facilitator resulting in an increase of species richness and density. However, our indicator species analysis showed that the species on the Bracken site were exclusively wind-borne. While the Shrub site had an attractive vegetation structure for stimulating the activity of birds and thus may facilitate seed dispersal of woody species as described in other studies (Vieira et al. 1994; Holl 1998b), the Bracken site was possibly less attractive for seed dispersers and thus experienced limited animal-dispersed seed availability. Several studies already have shown that seed availability is a major limiting factor in forest recovery (e.g. Gallegos et al. 2016). To assist succession on these sites, it may be appropriate to make them more attractive to seed dispersers through the installation of perches or planting of trees to increase the attractiveness of these sites. This has been shown to be effective in many cases (Holl et al. 2000; Hooper et al. 2005). Moreover, the shrubs provide microhabitat amelioration, which allows for an appropriate combination of light and shade for the germination, establishment and survival of seedlings as noted for other ecosystems (Vieira et al. 1994; Gómez-Aparicio et al. 2008).

Bracken fern species has been considered a barrier for regeneration due to its phytotoxic effects (Gliessman and Muller 1978; Marrs et al. 2000). However, Gallegos et al. (2015) found a facilitative effect for Clusia seedlings recruitment and potentially for other late-successional species; Günter et al. (2009) demonstrated in a reforestation experiment in our study area that seedlings of *Cedrela montana* Moritz ex Turcz had an acceptable development under bracken fern and Douterlungne et al. (2008) showed in the rain forest of Chiapas in Southern Mexico that *Ochroma pyramidale* (Cav. ex lam.) could also be established well in *Pteridium aquilinum* L. Kuhn. On the Bracken site our results showed that beneath *P. arachnoideum* cover the recruitment of species richness and density increased across time mainly in the last period of monitoring. Potentially, bracken fern canopy provides shade and protection to seedlings against high irradiation, rain and wind, and the root density is lower compared to grasses. However, there is evidence that the structural development of vegetation at the Bracken site is still behind the shrub site as the area is dominated by wind-dispersed pioneer species.

Based on prevailing effects of facilitation, the Bracken and Shrub sites show more dynamic woody species recruitment. Nevertheless, on bracken and especially pasture sites efforts should be put into the recruitment of animal-dispersed woody species; technical assistance such as the installation of perches, enrichment planting or direct seeding may be required.

Effects of removal of competing ground vegetation on woody diversity

The weed removal treatment applied in this study was not suitable for accelerating the natural succession process in terms of species diversity. These findings are in line with studies in Brazil (Sampaio et al. 2007) and Panama (Hooper et al. 2005). The mechanical treatment as applied was not able to compensate the higher growth rates of both species *S. sphacelata* and *P. arachnoideum*, which in turn impede the recruitment of woody species.

Interestingly, our study demonstrated that manual treatment on the Bracken and Shrub sites can actually be ineffective to species recruitment and on density. The herbaceous competing vegetation on the Shrub site was heterogeneous and less dense than the vegetation on the Bracken and Pasture sites. Obviously, even with high attention during the cleaning process it is possible that also emerging seedlings have been affected by the treatment. However, the competing vegetation was only carefully cut back to reduce their competiveness and not completely eliminated in order to allow for the development of emerging seedlings. We therefore suggest that our manual treatment is inappropriate for these conditions, and should not be used. Although we cannot state that other treatments would not be effective as, for example, herbicides have proven to be apt for reducing competition stress in other cases (Griscom et al. 2009), although in restoration, only herbicides with relative low toxicity and low persistence are acceptable (Davy 2002). Glyphosate, used successfully in a reforestation experiment, was found to be the most appropriate grass-elimination treatment to improve tree growth on pastures (Weber et al. 2008). In general, a higher frequency of manual weeding or chemical application could be more effective but unsuitable in terms of cost efficiency.

Pathways of succession

Many degraded lands can be restored along successional pathways (Suding et al. 2004), and two successional trajectories have been described in the literature such as divergent, which emphasized the importance of early successional species interactions and topography (Harvey and Holzman 2014) and convergent may occur later in succession with the arrival of late successional species (Capers et al. 2005). In this context, over the 4 years of monitoring in this study, the floristic composition of the Shrub and Bracken sites has become more similar due to a long period since the last anthropogenic fire event. However, ordination shows that the two sites, rather than following the same successional trajectories, are following parallel ones. So far it is still not clear whether the vegetation at the different sites is converging towards a common ‘final state’.

In the case of the Pasture site, conversely, shows a much slower recovery and it could either follow an inhibition model according to Connell and Slatyer (1977) or a model of deflection or arrested succession generated by *S. sphacelata* (Sarmiento 1997). Bakker et al. (1996) showed that successional pathways, dynamics and speed of recovery are inextricably linked to site history. Therefore, the presence of *S. sphacelata* is probably not the only reason for the low succession, and the previous intensive grazing and probable soil compaction through cattle trampling may also be contributing to the distinct successional trajectory.

Based on a 4-year period of monitoring in our study area, we conclude that it is not possible to determine if our Pastures and Bracken sites have diverging or converging diachronic successional pathways due to the little-advanced stages of succession However, the target of restoration or possible multiple alternative outcomes need to be defined (Newton and Cantarello 2015).

Conclusions

Land use history and the current vegetation strongly affect woody species recruitment on degraded areas in our study area corresponding a tropical mountain forest ecosystem. Facilitation effects are prevailing in areas with established vegetation of shrubs, whereas competition effects are strong on recently abandoned pastures and affect species diversity, density and successional pathways. Recruitment of animal-dispersed species on the shrub site emphasizes the importance of perch trees for reaching late successional stages. Bracken provides better suitable conditions than grasses on open pastures for faster tree recovery, however limited to wind dispersed species. Pastures dominated by *S. sphacelata* in turn reduced the dynamics of species recruitment drastically. Manual weeding seems not always be a suitable practice for accelerating restoration process. Management and conservation efforts should therefore focus on (1) planting *S. sphacelata* only on sites where long term management is possible, (2) improving pasture management on these sites to avoid abandonment, (3) making use of bracken for tree recovery and (4) including perch trees establishment into restoration strategies.

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Appendix

See Table 5.

Table 5 List of woody indicator species showing a comparison between 0 and 48 months per site with highest significance ($p < 0.05$)

Family	Species	Dispersal	Life-form	Natural forest	*p* value					
					0 months			48 months		
					P	B	S	P	B	S
Aquifoliaceae	*Ilex* sp.	Bird	Treelet	P						0.011
Asteraceae	*Ageratina dendroides* (Spreng) R.M. King & H. Rob	Wind	Shrub	A			0.001			0.004
Asteraceae	*Ageratina* sp.	Wind	Shrub	A				0.001		
Asteraceae	*Baccharis brachylaenoides* DC.	Wind	Shrub	A					0.04	
Asteraceae	*Baccharis macrantha* Kunth	Wind	Shrub	A						0.021
Asteraceae	*Baccharis latifolia* (R&P) Pers.	Wind	Shrub	A	0.001			0.009		
Asteraceae	*Baccharis* sp.	Wind	Shrub	A						0.009
Asteraceae	*Baccharis obtusifolia* Kunth	Wind	Shrub	A		0.002				
Asteraceae	*Baccharis* sp1	Wind	Shrub	A					0.001	
Asteraceae	*Baccharis tricuneata*	Wind	Shrub	A					0.002	
Asteraceae	*Vernonia* sp2	Wind	Shrub	A					0.024	
Caprifoliaceae	*Viburnum pichinchensis* Benth	Bird	Tree	A						0.003
Clethraceae	*Clethra fagifolia* Kunth	Wind	Tree	A						0.003
Clusiaceae	*Clusia* sp1	Bird	Tree	P						0.013
Clusiaceae	*Clusia* sp2	Bird	Tree	P						0.008
Cyatheaceae	*Cyathea* sp.	Wind	Treelet	P			0.004			
Ericaceae	*Macleania poortmannii* Drake	Bird	Tree	A						0.001
Ericaceae	*Vaccinium floribundum* H.B.K.	Bird	Shrub	A						0.001
Euphorbiaceae	*Alchornea pearcei* Britton ex Rusby	Wind	Tree	P						0.008
Gentianaceae	*Macrocarpaea* sp.	Bird-bat	Treelet	P						0.001
Grosilariaceae	*Escallonia paniculata* (Ruiz & Pav.) Roem. & Schult.	Wind	Treelet	A					0.022	
Lauraceae	*Persea* sp.	Bird	Tree	P						0.03

Table 5 continued

Family	Species	Dispersal	Life-form	Natural forest	*p* value					
					0 months			48 months		
					P	B	S	P	B	S
Melastomataceae	*Brachyotum campanulare* (Bonpl) Triana	Wind	Shrub	A	0.019					0.001
Melastomataceae	*Monochaetum lineatum* (D. Don) Naudin.	wind	shrub	A					0.002	
Melastomataceae	*Tibouchina laxa* (Desv.) Cogn	Wind	Shrub	A			0.003			0.032
Melastomataceae	*Miconia* sp.	Bird	tree	P			0.044			
Myrsinaceae	*Myrsine coriacea* (Sw.) R. Br. Ex Roem. & Schult.	Bird	Treelet	P			0.001			0.001
Rubiaceae	*Palicourea* sp1.	Bird	Treelet	P						0.001
Rubiaceae	*Palicourea* sp2.	Bird	Treelet	P			0.001			
Proteaceae	*Roupala montana* Aublet	Wind	Tree	P					0.004	
Rosaceae	*Hesperomeles obtusifolia* Pers.	Bird	Tree	A						0.007
Rubiaceae	Palicourea anceps Standl	Bird	Treelet	P						0.001

The reference ecosystem Reserva Biológica San Francisco: *P* present, *A* absent

Successional sites: *P* pasture, *B* bracken, *S* shrub

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