

# The potential to restore native woody plant richness and composition in a reforesting landscape: a modeling approach in the Ecuadorian Andes

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## Abstract

**Context** Natural regenerating forests are rapidly expanding in the tropics. Forest transitions have the potential to restore biodiversity. Spatial targeting of land use policies could improve the biodiversity benefits of reforesting landscapes.

**Objective** We explored the relative importance of landscape attributes in influencing the potential of tree cover increase to restore native woody plant biodiversity at the landscape scale.

**Methods** We developed land use scenarios that differed in spatial patterns of reforestation, using the Pangor watershed in the Ecuadorian Andes as a case study. We distinguished between reforestation

through natural regeneration of woody vegetation in abandoned fallows and planted forests through managed plantations of exotic species on previously cultivated land. We simulated the restoration of woody plant biodiversity for each scenario using LANDIS-II, a process-based model of forest dynamics. A pair-case comparison of simulated woody plant biodiversity for each scenario was conducted against a random scenario.

**Results** Species richness in natural regenerating fallows was considerably higher when occurring in: (i) close proximity to remnant forests; (ii) areas with a high percentage of surrounding forest cover; and (iii) compositional heterogeneous landscapes. Reforestation at intermediate altitudes also positively affected restoration of woody plant species. Planted exotic pine forests negatively affected species restoration.

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**Conclusions** Our research contributes to a better understanding of the recolonization processes of regenerating forests. We provide guidelines for reforestation policies that aim to conserve and restore woody plant biodiversity by accounting for landscape attributes.

**Keywords** Biodiversity restoration · Landscape planning · LANDIS-II · Planted forest · Reforestation

## Introduction

Although tropical deforestation continues at a rapid rate, there is also evidence of a regrowth of tropical and subtropical forests in some regions. Regrowth occurs in various ways. For example, through regenerating forests that naturally establish after human or natural disturbance of the original forest vegetation (Chokkalingam and de Jong 2001; Chazdon 2014) or planted forests composed of trees established through planting of native or exotic species (FAO 2015). To date, we still lack an accurate estimate of the extent of regenerating or planted tropical forests (but see Asner et al. 2009; Meyfroidt and Lambin 2011). Numerous studies have emphasized the critical importance of regenerating forests in tropical landscapes (Dunn 2004; Chazdon 2008; DeClerck et al. 2010), but have also emphasized the differences between forest transition pathways to restore biodiversity and ecosystem functions (Meyfroidt and Lambin 2011; Chazdon 2014).

In Ecuador, land reforms and governmental programs (e.g., the payment for carbon sequestration program PROFAFOR) have stimulated forest plantations from the 1960s onwards, leading to the conversion of large areas of natural grasslands to exotic pine plantations in the highlands (Farley 2007, 2010). Economic and demographic forces, such as land abandonment with economic development, have also favored natural regeneration of tropical forests (Rudel et al. 2005; Lambin and Meyfroidt 2010) and have been observed in the Ecuadorian Andes (Balthazar et al. 2015). Ecuadorian conservation policies (e.g., the payment for ecosystem services program SocioBosque) have started to recognize the role of forest regrowth at the landscape level and will incorporate reforestation programs in the future (de Koning et al. 2011).

Natural regenerating and planted forests affect the spatial configuration and composition of landscapes and therefore habitat distribution. Landscape structure has been suggested as an important factor that determines the effectiveness of local biodiversity conservation management in human-modified landscapes (Tscharntke et al. 2012). Even though landscape fragmentation has been recognized as a key factor in biodiversity loss (Fischer and Lindenmayer 2007), the effect of landscape patterns on restoration of biodiversity and ecosystem functions in reforesting landscapes is still not well understood (Hall et al. 2012; Leite et al. 2013; Melo et al. 2013). Well-designed approaches of reforestation policies could improve natural regeneration of native species at a landscape scale.

The objective of this study was to better understand the relative importance of landscape attributes in influencing the potential of tree cover increase to restore native woody plant richness and composition at the landscape scale. We focused on human-modified landscapes in the Ecuadorian Andes, where extensive farming and grazing takes place. We used a process-based vegetation model to simulate forest cover and species dynamics. We distinguished between reforestation through woody vegetation gain by natural, unassisted regeneration of abandoned fallows, and planted forests through managed plantations of exotic species on previously cultivated lands. We focused on the richness and composition of woody plants, as the diversity and structural characteristics of vegetation in regrowth forests were important determinants of faunal assemblages (Evelyn and Stiles 2003; Kanowski et al. 2006; Bowen et al. 2007). This research provides guidelines for reforestation policies that aim to enhance biodiversity restoration in human-modified landscapes.

## Background

Many studies that have explored the effects of landscape patterns on species richness have been based on costly and time consuming fieldwork, carried out over short time periods (<5 years). In the tropics, available data reflect a sampling bias towards young regenerating forests (Chazdon et al. 2009b) and long-term datasets are scarce (Chazdon et al. 2009a; Gardner et al. 2009). Model simulations allow

considerably more experimentation with various landscape patterns and over much longer time periods than possible in the field.

In this study, we used the spatially explicit landscape simulation model LANDIS-II (Scheller et al. 2007) to test various hypotheses on landscape factors influencing the recovery of woody species richness and composition resulting from tree cover increase in a tropical landscape. LANDIS-II is a well-established model that simulates the dynamics of forested landscapes over large spatial scales by incorporating ecological processes, such as succession, disturbance, and seed dispersal. In Latin America, LANDIS-II has been used to support conservation planning in a dry-land environment in Chile (Newton et al. 2011), to assess the potential for forest restoration in two Mexican landscapes under different disturbance regimes (Cantarello et al. 2011), and to predict the spatial extent of forest restoration (Birch et al. 2010). Thompson et al. (2011) showed that LANDIS-II could simulate forest to non-forest transitions.

The ecological value of forest regeneration is influenced by many factors. Beyond the local site characteristics (i.e., climate, soil fertility), landscape dynamics affect the initial establishment, species composition, and persistence of regenerating forests (Chazdon et al. 2009b). Landscape attributes (e.g., distance to forest remnants, local forest cover, heterogeneity of surrounding land covers) and temporal dynamics (e.g., time since abandonment) have a strong influence on the reforestation trajectory (Chazdon 2003). We tested seven hypotheses based on the literature (Table 1), which are justified here.

Local forest regrowth is linked with features of the surrounding landscapes through source populations

and processes of seed dispersal. The extent and distribution of forest cover in the surrounding landscape serves as the external ecological memory and influences the recruitment of forest species during recolonization (Chazdon 2014). In previous studies, the presence of old-growth forest remnants promoted the reassembly of tropical communities (Norden et al. 2009). Proximity to mature forests was particularly important during forest regrowth, as remnant vegetation provided a seed source (Guariguata and Ostertag 2001; Mesquita et al. 2001; Günter et al. 2007). The lack of dispersal of forest seeds was found to be one of the most important barriers to the restoration of tropical montane forest on abandoned pastures (Holl et al. 2000). We thus expect that the recovery of species richness and composition in regenerating fallows positively relates to a greater proximity to natural forest remnants (*hypothesis 1*) and a higher percentage of surrounding natural forest cover (*hypothesis 2*).

The diversity of different natural land covers (i.e., compositional heterogeneity) is also important during species regeneration (Gardner et al. 2009). Fahrig et al. (2011) suggested that biodiversity is expected to increase through the accumulation of species as more natural cover types are added to the landscape. Compositional heterogeneity was a key component for explaining landscape species richness (Wagner et al. 2000). We expect that a higher compositional heterogeneity of surrounding natural land covers positively affects the recovery of species richness and composition in regenerating fallows (*hypothesis 3*).

Island biogeography and metapopulation theories predict that the largest patches hold the most species as a

**Table 1** Overview of the hypotheses tested in this study

Hypothesis	Landscape attribute
1	The recovery of woody species richness and composition in regenerating fallows are positively correlated with ... ...proximity to natural forest remnants
2	...cover percentage of surrounding natural forest remnants
3	...compositional heterogeneity of surrounding natural land covers
4	...the size of regenerating patches
5	...time since abandonment of regenerating patches
6	The recovery of woody species richness and composition in regenerating fallows is negatively correlated with ... ...the altitude of regenerating patches
7	...planted forest using exotic pine species

result of lower extinction rates (MacArthur and Wilson 1967; Hanski 1999). In highly fragmented tropical landscapes, the size of remnant forest patches was positively related to plant species density (Arroyo-Rodríguez et al. 2009; Hernández-Stefanoni et al. 2011). We expect that a larger size of regenerating forest patches positively affects the recovery of species richness and composition (*hypothesis 4*).

It has been shown that plant species richness increased over time during forest regrowth (Guariguata and Ostertag 2001; Barlow et al. 2007; Dent and Wright 2009; Norden et al. 2009), making the age structure of regenerating forests an important determinant of landscape-level biodiversity. At initial stages of reforestation, typical old-growth species and endemic forest specialists may be missing, but they might be able to establish later (Chazdon 2003). We expect that time since abandonment of regenerating fallows positively affects the recovery of species richness and composition (*hypothesis 5*).

Altitude is a well-known driver of compositional variation in Andean vegetation (Jørgensen and Ulloa Ulloa 1994). Individuals of the same species have been found to differ in growth rate across their altitudinal ranges due to changes in temperature (Rapp et al. 2012). Recovery rates in cloud forests might lag behind due to lower temperatures at higher altitudes that cause trees to grow slowly. We expect that a higher elevation of regenerating abandoned fallows negatively affects the recovery of species richness and composition (*hypothesis 6*).

Finally, studies showed that the ecological benefits of plantations depend largely on the land cover they replace and whether planted trees are native or introduced species (Bremer and Farley 2010). Most exotic forest plantations established in high altitude grasslands in Ecuador negatively affected the water retention and carbon storage capacity of páramo soils (Molina et al. 2012; Farley et al. 2013) and offered little value for biodiversity conservation (Hofstede et al. 2002). We expect that planted forests using exotic pine species negatively affects the recovery of species richness and composition in previously cultivated areas (*hypothesis 7*).

We simulated restoration of woody plant richness and composition using LANDIS-II over a series of land-use scenarios that explored a range of variation in the seven key landscape attributes introduced above (Table 1). This approach facilitated the comparison of

different landscape architectures of reforestation to evaluate the relative importance of landscape attributes on biodiversity restoration.

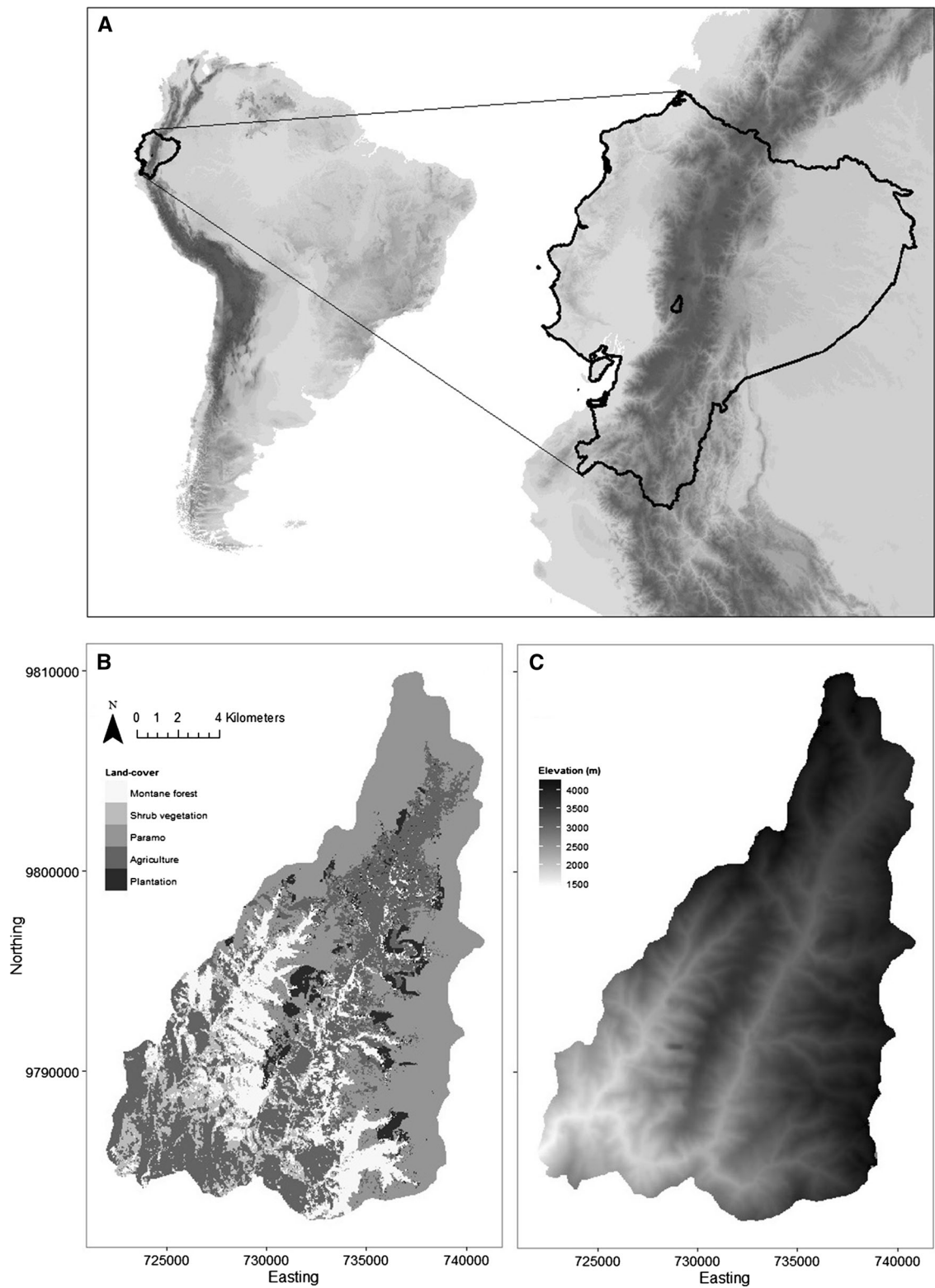
## Data and methods

### Study area

The Pangor watershed (78°50′–79°01′W, 1°43′–1°58′S) located in the Chimborazo province is a headwater basin of ~282 km<sup>2</sup> and ranges from 1431 to 4333 masl (Fig. 1a). The mean annual precipitation is ~1400 mm and the topography is characterized by steep slopes, with over half of the catchment above 25°. Soils developed on volcanic ash deposits (mainly Andosols) and are characterized by a high water retention capacity and soil organic matter content when undisturbed (Buytaert et al. 2005). However, these soils become susceptible to erosion when cleared or cultivated.

Temperature, precipitation, and solar radiation are strongly correlated with elevation, leading to an altitudinal zonation of vegetation observed throughout the Ecuadorian Andes. The treeless area above 3400 masl is covered by grass páramo (i.e., *pajonal*), mainly consisting of bunch grasses with scattered herbs and shrubs. Forests of *Polylepis* trees occur sporadically in this zone, supporting additional woody species. Grass páramos can support a high number of species and are considered natural vegetation cover, although scientists have claimed it is man-made through burning during the Holocene (White 2013), consequently lowering the historical treeline (Jørgensen and Ulloa Ulloa 1994). Below the treeline, upper montane forest (>3000 masl) and montane forest (<3000 masl) cover the catchment. Upper montane forest is characterized by contorted tree growth with many multi-stemmed trees or giant shrubs. Montane forest (i.e., Andean cloud forest) is composed of a rich diversity of taller trees cover by diverse epiphyte flora and lianas.

Balthazar et al. (2015) highlighted a shift from net deforestation to net reforestation in the Pangor watershed in the early 1990s based on a 50-year time series consisting of aerial photographs and satellite images. Most of the lowland in the catchment has been cleared of its natural vegetation for small-scale agriculture of mainly beans, potatoes, and maize, while extensive



**Fig. 1** a Location of the Pangor watershed in Ecuador; b Land-cover classification; c Digital elevation model

grazing occurs on the high altitude grasslands. Since the late 1980s, pine plantations were established in the higher parts of the catchment (>3200 masl), after being promoted by governmental programs that linked the Ministry of Agriculture with rural landowners (Farley 2007, 2010). Approximately five percent of the watershed was covered with pine plantations by 2009 (Vanacker et al. 2013). Additionally, some abandoned agricultural lands were left for natural regeneration (Balthazar et al. 2015).

### Forest landscape model

LANDIS-II is a stochastic, spatially-explicit, raster-and process-based model that simulates the dynamics of forested landscapes on large spatial and temporal scales by incorporating ecological processes, such as succession, disturbance, and seed dispersal (Scheller et al. 2007). Species composition and succession is driven by the user-defined life history characteristics of each modeled species (i.e., longevity, minimum age at reproduction, shade tolerance, minimum/maximum seed dispersal distances, and sprout probability) and their establishment coefficient. This coefficient governs the probability of each species to establish in different subdivisions of the landscapes that are homogeneous in environmental conditions (i.e., ecoregions). For each cell, the presence and absence of 10-year age cohorts is monitored. A more detailed description of LANDIS-II can be found elsewhere (He et al. 1999; Mladenoff 2004; Scheller et al. 2007; <http://www.landis-ii.org>).

### Field survey data

To determine the floristic composition across the Pangor watershed, we collected species data in September and October 2013 from twelve 0.02 ha transects (40 × 5 m) (Table S1). These transects were parallel to the contour lines of the slope in montane forest (n = 3), upper montane forest (n = 2), natural regenerating forest (n = 2), pine plantations (n = 4), and páramo (n = 1). Jorge Caranqui collected additional species data in 2007 from five 0.02 ha transects (50 × 4 m) in montane forest (*unpublished data*), resulting in a total of eight montane forest plots. Plots were selected using a subjective sampling approach, to identify sample units that are assumed to be representative of the entire population.

In each plot, plant height and diameter at breast height (DBH) for all woody plants >1 cm DBH were recorded. Based on collected specimens, all individuals were subsequently identified at the Herbario QCA at the Pontificia Universidad Católica del Ecuador. Plant species names and authorities were according to Jørgensen and León-Yáñez (1999). We excluded six individuals that could not be identified to genus level.

### Model parameterization

LANDIS-II is designed to accept raster imagery as spatially explicit input. The required input maps are an ecoregion map that describes the ecological conditions affecting species establishment and an initial communities map that describes the distribution and age of cohorts for each species at the onset of simulations. All maps were produced and manipulated using ArcGIS 10.2.2 (© 2014 ESRI Inc., Redlands, California, USA).

### Ecoregions

Vegetation zonation in the Ecuadorian Andes is strongly related to altitude. We selected the elevation zonation as proposed by Jørgensen and Ulloa Ulloa (1994). We generated a total of 11 active ecoregions by overlaying a Digital Elevation Model and a beam solar irradiation map (Table S2). All regions above 3,700 masl and all agricultural raster cells were inactive during simulations as they mainly consisted of herbaceous and small shrub vegetation in most of our study area. The species establishment probabilities were derived from MaxEnt models (Phillips et al. 2006) as the average probability of occurrence for each species in each ecoregion. Input data for these models included species occurrence data from the MOBOT Tropicos<sup>®</sup> database (©2014 Missouri Botanical garden, USA) and bioclimatic variables extracted from the Worldclim database (Hijmans et al. 2005).

### Initial communities

A land cover map with a spatial resolution of 30 m was made for 2010 based on a supervised classification method using Worldview-2 imagery, with an average accuracy of 80.4 % and a Kappa coefficient of 77.5 % (Marie-Pierre de Wouters and Vincent Balthazar—*unpublished data*). Six land cover types were

identified: (1) natural forest remnants (i.e., cloud and upper montane forest); (2) shrub vegetation mainly characterized by natural regeneration; (3) sub páramo; (4) grass páramo; (5) agriculture; and (6) pine plantations (Fig. 1).

The initial distribution, composition, and age structure of forest communities for each cell in the landscape was determined by combining the land cover classification with the field survey data. We estimated ages of individuals by dividing the measured height with the maximum documented height, multiplied with the maximum documented longevity for each species.

### *Species attributes*

We selected a subset of the 19 most abundant species based on their importance value index, which is the sum of relative density, relative frequency, and relative dominance found during the field survey (Mishra 1968). For each modeled species, we extracted life history characteristics from the literature and from a consultation of local experts (Table S3).

### Scenarios

To explore the relative importance of landscape attributes on the re-colonization of biodiversity during reforestation, we developed alternative land-use scenarios that differed in the pattern of reforestation (Table 1). First, we estimated the rate of past natural regeneration based on post-classification change detection between land-cover classifications of two satellite imagery for 1991 and 2009 (Balthazar et al. 2015), using Markov Chain Analysis (MCA) within the Land Change Modeler (LCM) in IDRISI Taiga v.17.01 (©2015 Clark Labs, Clark University, Worcester, USA). We projected the area of natural regenerating forests from 2010 to the year 2055 to ~943 ha (i.e., 10,476 raster cells). All natural regeneration during simulations took place in former agricultural raster cells and at equal time intervals of 15 years (i.e., year 2010, 2025, and 2040) to disintegrate the influence of time since onset of regeneration on species richness.

The spatial allocation of raster cells under reforestation varied for each scenario, altering the: (i) proximity to remnant forest; (ii) percentage of surrounding forest cover; (iii) compositional heterogeneity of

surrounding natural land-cover; (iv) patch size; (v) elevation; and (vi) type of reforestation (i.e., planted pine forests). We created one random reforestation scenario with a similar area of reforestation that served as a reference to which all other scenarios were compared. The proximity to remnant forest was calculated as the Euclidean distance to the nearest forested cell. The percentage of forest cover in the surrounding landscape was calculated in a 200 m radius surrounding the focal cell. Compositional heterogeneity was determined as the Simpson's diversity index, which represents the probability that any two pixels selected at random were different patch types, calculated for a 200 m radius moving window using FRAGSTATS software V.4.2 (McGarigal et al. 2012). We varied patch size by increasing from 150 m to 250 m the buffer size in which reforestation occurred around randomly selected raster cells. For the plantation scenario, an age-cohort of pines was planted at the onset of regeneration at random locations across the landscape. We created a total of one random, one planted forest, and 15 reforestation scenarios (Table 2; Fig. S1).

We implemented the Base Harvest (v2.2) extension of LANDIS-II (Gustafson et al. 2000) to simulate reforestation during simulations. At each harvesting time step, raster cells identified for reforestation were completely harvested until the onset of reforestation (i.e., 2010, 2025, and 2040). Simulations were conducted for 55 years. Each scenario was replicated three times with a different random seed number to account for within-scenario stochasticity. The time steps were 5 years for tree succession and 1 year for the harvesting extension.

### Data analysis

The Age Cohort Statistics v1.0 extension of LANDIS-II generated raster maps for each time step containing for each pixel: (i) the minimum and maximum age across all species; (ii) the presence or absence of all species; and (iii) the total number of tree species. All output maps were analyzed using the raster package (Hijmans 2014) in R (R Development Core Team 2010). We recalculated species richness maps to contain only individuals >1 year.

At the landscape scale, we calculated the mean and standard deviations for the area in hectares containing a number of species and for the cover percentage of

**Table 2** Names and description of 17 scenarios simulated in LANDIS-II

Scenario name	Reforestation occurs ...
Random	...randomly on previously cultivated lands
Distance <200 m	...at an Euclidean distance to the nearest forested cell smaller than 200 m
Distance 200–400 m	...at an Euclidean distance to the nearest forested cell between 200 and 400 m
Distance >400 m	...at an Euclidean distance to the nearest forested cell larger than 400 m
Forest cover <50 %	...where the percentage forest cover in a 200 m radius lies between 0 and 50 %
Forest cover >50 %	...where the percentage forest cover in a 200 m radius lies between 50 and 100 %
Forest cover <30 %	...where the percentage forest cover in a 200 m radius lies between 0 and 30 %
Forest cover >30 %	...where the percentage forest cover in a 200 m radius lies between 30 and 100 %
Diversity index <50 %	...where the Simpson's diversity index in a 200 m radius is smaller than 0.5 (i.e., low compositional heterogeneity)
Diversity index >50 %	...where the Simpson's diversity index in a 200 m radius is larger than 0.5 (i.e., high compositional heterogeneity)
Patch size <	...in patch sizes with a diameter of maximum 150 m
Patch size >	...in patch sizes with a diameter of 150–250 m
Altitude <2400 m	...randomly at altitudes below 2400 masl
Altitude 2400–3000 m	...randomly at altitudes between 2400 and 3000 masl
Altitude 3000–3400 m	...randomly at altitudes between 3000–3400 masl
altitude >3400 m	... randomly at altitudes above 3400 masl
Plantation	... after planting an age-cohort of exotic pine trees randomly on previously cultivated lands

selected species over time for three repeated simulations of each scenario. We selected the following species for analysis, based on their life characteristics (e.g., shade-tolerance, seed dispersal limitations): *Aegiphila bogotensis*, *Baccharis latifolia*, *Boehmeria aspera*, *Clusia multiflora*, *Gynoxys* spp., *Hedyosmum luteynii*, and *Podocarpus glomeratus*.

We compared simulated species richness for reforesting fallows between each scenario and the random scenario using a pair matched case-comparison method. This approach accounts for the imbalance in co-variables (i.e., altitude, solar irradiance, time since abandonment) that influences species establishment during simulations. We conducted a genetic matching with replacement in R (Sekhon 2011). This algorithm found the optimal pair of matching that achieves covariance balance. We assessed the causal effect of a given landscape attribute on the simulated species richness based on matched data by comparing means of each scenario against the random scenario, using Wilcoxon-Mann-Whitney tests. In the subsequent results, we only included the results for scenarios that showed a significantly different average species richness compared to the random scenario for the

matching analyses. These scenarios are indicated in the text as 'significant scenarios'. All other results are included in the appendices and are indicated in the text as 'non-significant scenarios'.

Descriptive statistics were used to calculate the mean cover percentage of reforesting fallows containing a number of species. In addition we calculated  $\alpha$ -, and  $\beta$ -diversity values to assess the changes in landscape biodiversity, using the vegan package in R (Oksanen et al. 2007). We calculated  $\alpha$ -diversity as the mean species richness in reforesting raster cells (Whittaker 1972) and  $\beta$ -diversity as the dissimilarity between two reforesting raster cells based on counts at each cell, using the Bray-Curtis index (Bray and Curtis 1957). We also calculated the cover percentage of selected species over time for reforesting fallows in each scenario.

## Results

### Field survey

A total of 80 woody species were encountered in the field sites, although taxonomic uncertainty over



some genera led to congeneric species being grouped under the same species life history characteristics in the model. The most important tree species were *Hedyosmum luteynii* and *Aegiphila bogotensis* in montane forest, *Berberis* spp. and *Brachyotum ledifolium* in upper montane forest, and *Miconia* spp. and *Baccharis latifolia* in regrowth forest (for all species encountered, see Table S4). A total of 49 species were found in montane forest with an average richness of 12 species per plot. Natural regenerated forests were species rich with ~15 species per plot. However, species composition did not resemble montane forests completely, containing more shade-intolerant pioneer species. In the páramo plot, we found a total of 12 woody species. Pine plantations contained little or no undergrowth. We encountered more than two shrub species only in one plantation that was less densely planted with pines and located in close proximity to remnant forest.

#### Species restoration, proximity, and cover percentage of remnant forest patches

Consistent with hypotheses 1 and 2, we found significantly higher species richness for regenerating fallows located within 400 m from forest remnants and surrounded by more than 30 % cover of forest remnants compared to random reforestation ( $P < 0.05$ , two-sided Wilcoxon-test; Fig. 3). For these scenarios,  $\alpha$ -diversity values were high but  $\beta$ -diversity values were low and decreasing, indicating high mean species richness and a small differentiation between species occurring in fallows (Fig. 5). When forest cover dropped below 30 %, species richness recovery in natural regenerating forests was significantly lower ( $P < 0.05$ , two-sided Wilcoxon-test; Fig. 3) and more natural regenerating forests remained uncolonized (Fig. 4).

Simulated species composition of regenerating fallows resembled natural forests more when occurring in the proximity to natural forest remnants and in areas with a high percentage of remnant forest cover in the surrounding. In these scenarios, montane forest species, such as *A. bogotensis*, *C. multiflora*, *H. luteynii*, and *P. glomeratus*, were present in a larger number of regenerating fallows compared to other scenarios (Fig. 6a, d, f, h).

#### Species restoration and compositional heterogeneity

Consistent with hypothesis 3, we found significantly higher species richness in regenerating fallows with high compositional heterogeneity of surrounding natural cover types compared to random reforestation ( $P < 0.05$ , two-sided Wilcoxon-test; Fig. 3). Regenerating fallows located in compositional heterogeneous surroundings were increasingly dissimilar in species over time (Fig. 5b), indicating enhanced biodiversity at the landscape level (Fig. 2). These regenerating fallows were more often occupied by species typical of montane (Fig. 6a, d, h), shrub (Fig. 6c), and páramo (Fig. 6e) vegetation.

#### Species restoration and patch size

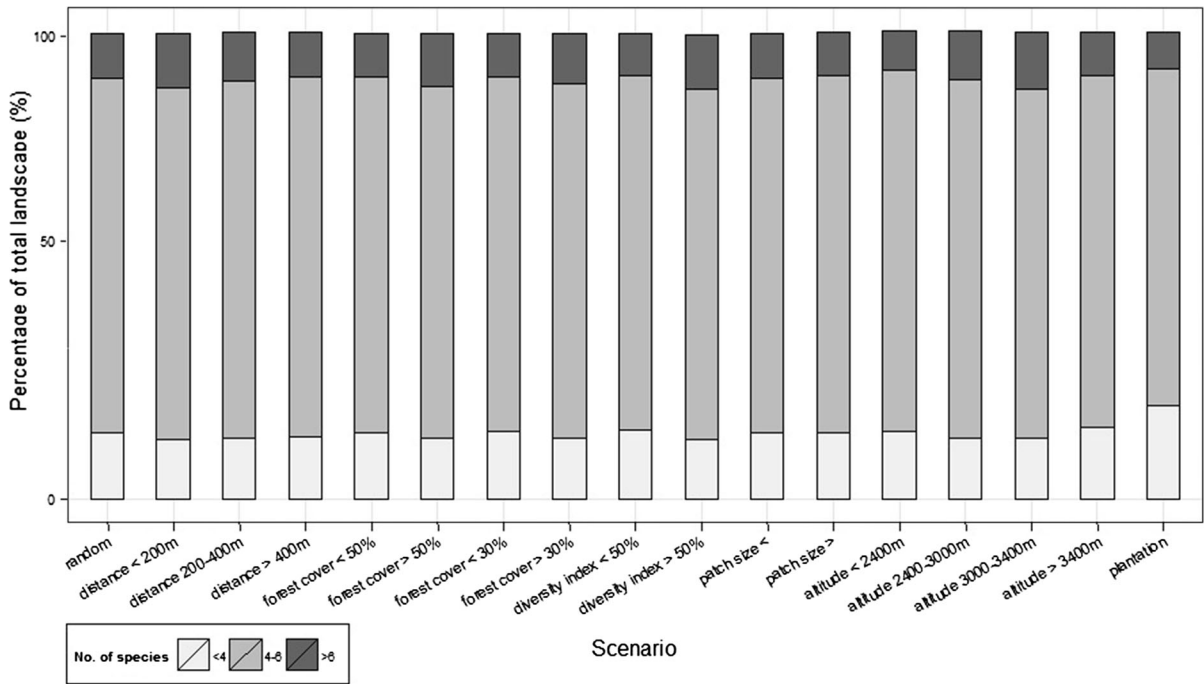
Contrary to hypothesis 4, our simulations showed no significant difference between the average species richness of regenerating forest of either small or large patch sizes compared to random reforestation (Fig. 3). Patch size scenarios also did not differ in terms of species richness at the landscape scale (Fig. 2) or recolonization dynamics over time (Fig. S3).

#### Species restoration over time

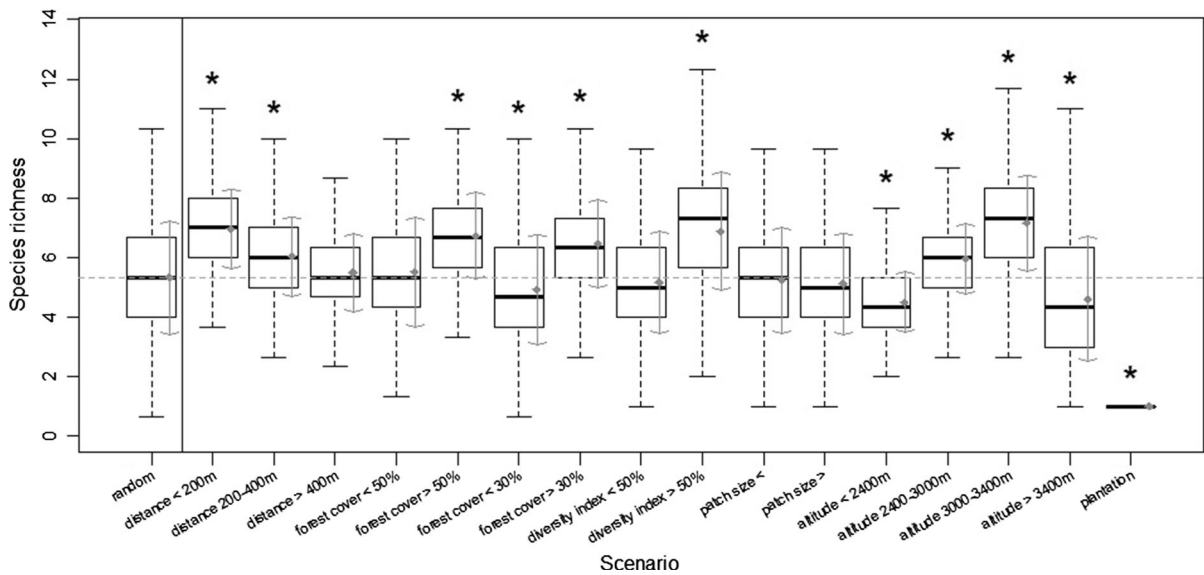
Species establishment in abandoned fallows was fast during all natural regeneration scenarios (Fig. 4). Consistent with hypothesis 5, most species rapidly increased their cover percentage in fallows after abandonment in all scenarios, except for the plantation scenario (Fig. 6). The presence of short-lived, shade-intolerant shrub species declined several decades after colonization (Fig. 6c, e), due to increasing levels of simulated shade during recolonization. This decline resulted in a decrease in species richness over time, shown by diminishing  $\alpha$ -diversity values for all scenarios (Fig. 5a).

#### Species restoration and altitude

Consistent with hypothesis 6, species richness in regenerating fallows was significantly lower at high altitudes (>3400 masl) and significantly higher at intermediate altitudes (between 2400 and 3400 masl) compared to random reforestation ( $P < 0.05$ , two-

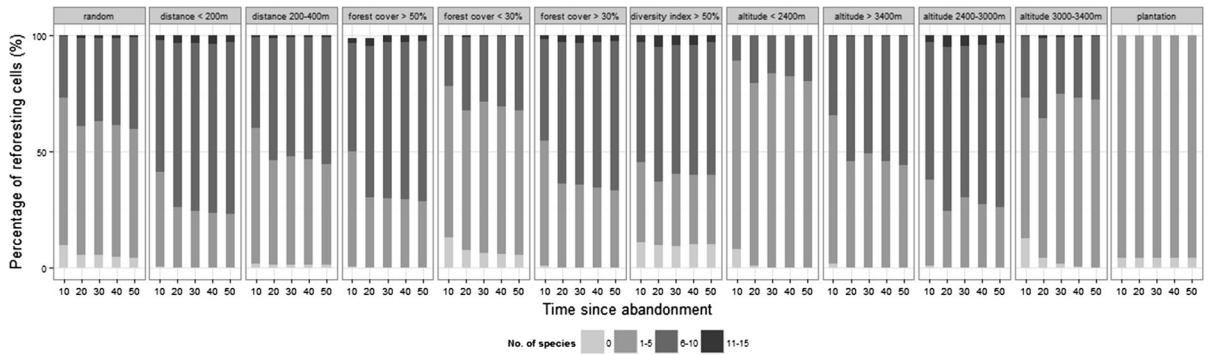


**Fig. 2** The percentage of the total landscape containing a number of woody species for all scenarios after 55 years of simulation. The location and type of reforestation affected the distribution of species richness at a landscape scale



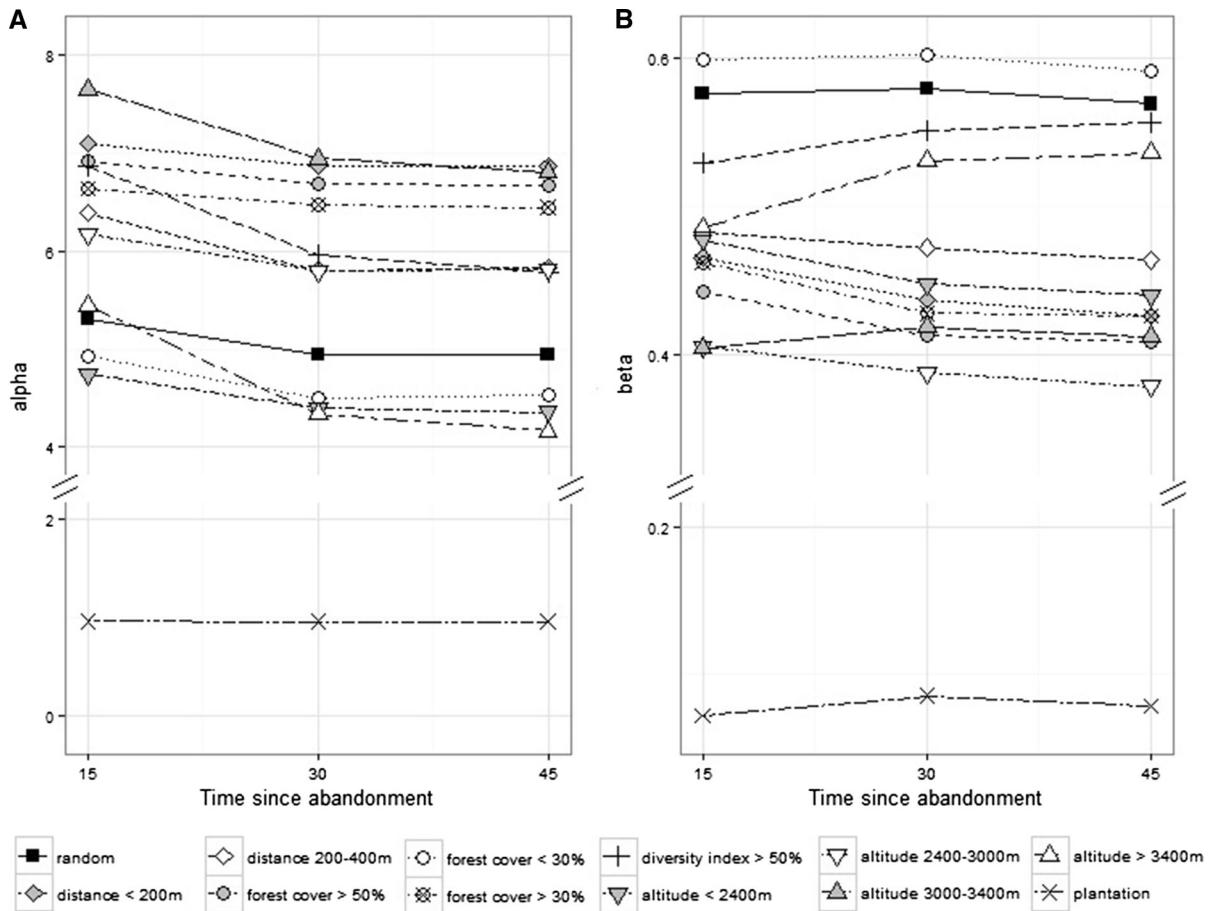
**Fig. 3** Boxplot showing the median, 25–75 % quartiles, and non-outlier ranges (in black), and the average and standard deviations (in grey) of simulated species richness after 55 years in reforesting fallows over three runs for each scenario. The horizontal dashed line indicates average species richness for the random scenario. Compared to the random scenario, average species richness was significantly higher for the

distance < 200 m, distance 200–400 m, forest cover > 50 %, forest cover > 30 %, diversity index > 50 %, altitude 2400–3000 m, and altitude 3000–3400 m scenarios and significantly lower for the forest cover < 30 %, altitude < 2400 m, altitude > 3400 m, and plantation scenarios. Significant differences are indicated by asterisks ( $P < 0.05$ , two-sided Wilcoxon-test)



**Fig. 4** The percentage of reforesting falls containing a number of woody species over time since abandonment for significant scenarios. Re-colonization of abandoned agricultural lands was dynamic during simulations. In particular, the

distance < 200 m, forest cover > 50 %, forest cover > 30 %, diversity index > 50 %, and altitude 3000–3400 m scenarios indicated a relatively large area that contained a large number of species



**Fig. 5** The development of the simulated **a** mean species diversity per cell (i.e.,  $\alpha$ -diversity) and **b** differentiation among these sites (i.e.,  $\beta$ -diversity) over time for significant scenarios.  $\alpha$ -Diversity decreased over time for all scenarios, whereas  $\beta$ -

diversity increased for diversity index > 50 %, altitude 3000–3400 m, and altitude > 3400 m scenarios, whereas it decreased for the remaining scenarios. Note the discontinued y-axis

sided Wilcoxon-test; Fig. 3). Contrary to hypothesis 6, however, we found significant lower species richness for regenerating fallows located below 2,400 masl compared to random reforestation ( $P < 0.05$ , two-sided Wilcoxon-test; Fig. 3), because the lower basin of the catchment has been almost completely cleared of natural forest remnants. Regenerating fallows located between 3,000 and 3,400 masl showed the highest  $\alpha$ -diversity values (Fig. 5a). Species associated with lower elevations, were more abundant in naturally regenerated forests below 2,400 m (Fig. 6c, g), while species that were able to establish and grow at high altitudes increased their cover percentage at intermediate altitudes (between 3000 and 3400 masl) (Fig. 6e, f, h).

#### Species restoration in planted forests

Consistent with hypothesis 7, we found significantly lower species richness for planted forest on previously cultivated land compared to random reforestation ( $P < 0.05$ , two-sided Wilcoxon-test; Fig. 3). Planted forests using exotic pine species prevented the establishment of all other species (Figs. 4, 5a, 6), leading to a diminished overall species richness at the landscape scale (Fig. 2).

## Discussion

#### Species restoration, proximity, and cover percentage of remnant forest patches

Our results demonstrate that remnant vegetation was an important seed source that determined the recovery of both species richness and composition during natural regeneration of abandoned fallows. Consistent with our results, other studies indicate a smaller numbers of individuals and species in abandoned fields under reforestation located further away from forests (e.g., Mesquita et al. 2001; Robiglio and Sinclair 2011). In the tropical mountain rainforest of Southern Ecuador, the total number of species found in natural regenerating forest decreased from 47 to 31 with increasing distance from the forest edge (Günter et al. 2007). In a review of more than 30 years of ecological restoration in Brazil, Rodrigues et al. (2009) have stated that the distance to the forest edge reduces species richness and diversity long after the

onset of forest regeneration. Our results support the idea that below a 20–30 % threshold of natural surrounding habitat, isolation becomes an important factor determining species richness (Andr en 1994; Fahrig 1998, 2003).

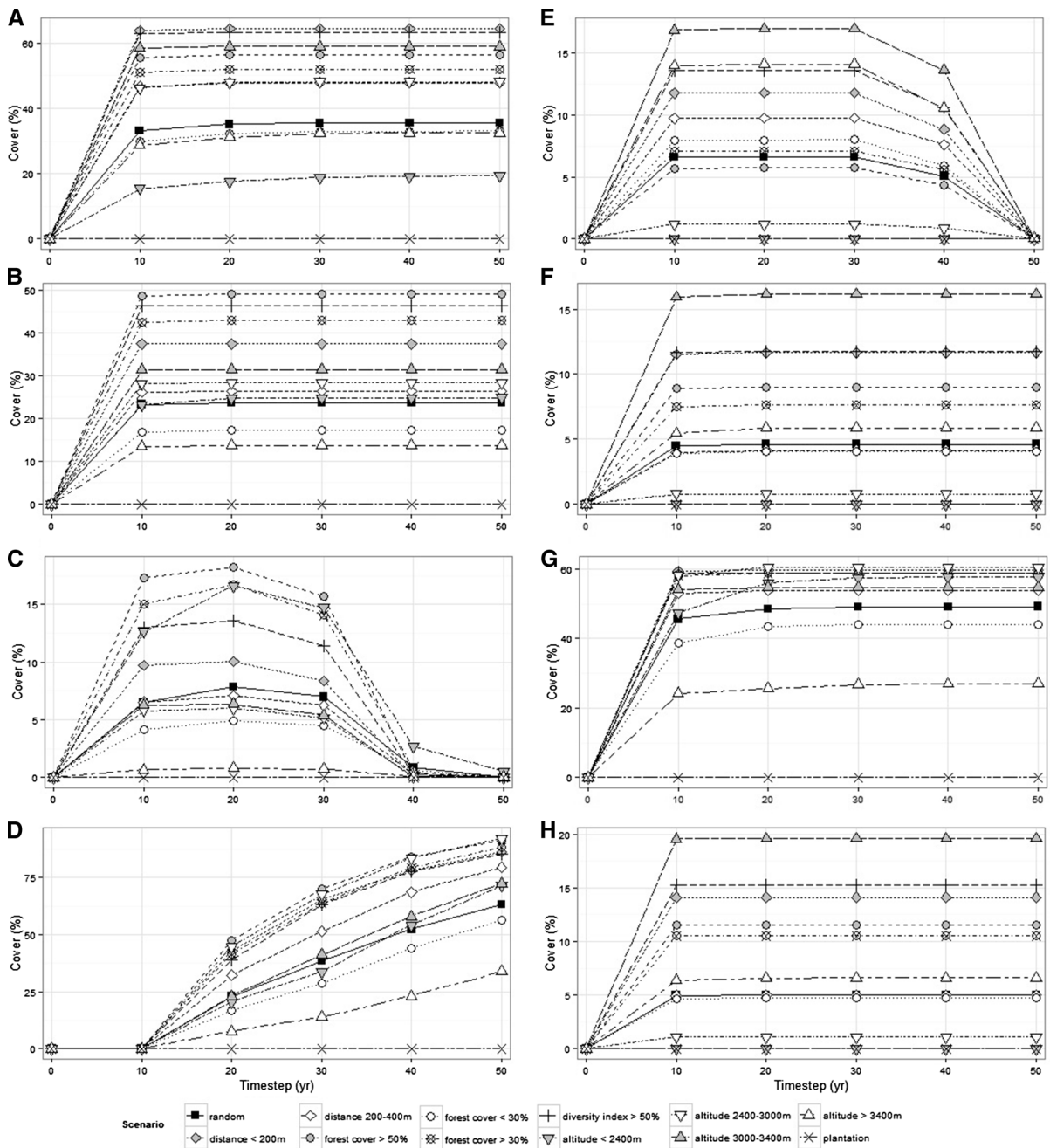
#### Species restoration and compositional heterogeneity

Compositional heterogeneity increased the recovery of species richness and composition during our simulations, due to the accumulation of species associated with different natural cover types. Similarly, Kumar et al. (2006) found that compositional heterogeneity (i.e., Simpson's diversity index) was positively correlated with native and non-native plant species richness for 180 plots in the Rocky Mountains. This effect was strongest at an intermediate spatial extent (240 m) (Kumar et al. 2006), which is comparable to the spatial scale of 200 m at which we found a positive effect of compositional heterogeneity on species richness. An increase in patch density (i.e., increased compositional heterogeneity), which resulted from low levels of land use, enhanced plant diversity in a tropical forest landscape in Mexico (Hern andez-Stefanoni et al. 2011). In a modeling approach, it was found that plant diversity was highest in heterogeneous landscapes with more small patches and low aggregation (Steiner and K ohler 2003).

Besides compositional heterogeneity, it has also been suggested that species diversity is positively correlated with an increasing complexity of patch shapes of different cover types (i.e., configurational heterogeneity) (Fahrig et al. 2011). In practice, these two dimensions are difficult to control independently (Fahrig et al. 2011). This study only focused on compositional heterogeneity. The nature of landscape heterogeneity-biodiversity relationships still needs further exploration. The effect of compositional heterogeneity on biodiversity likely depends on contextual factors, such as historical landscape patterns, time frame, and the nature of reforestation.

#### Species restoration and patch size

Our finding that patch size of regenerating fallows did not affect species richness or composition contradicts other studies. Several researchers have suggested that smaller patches support smaller populations, which



**Fig. 6** The cover percentage of natural regenerated fallows occupied by each selected species over time under significant scenarios. **a** *Aegiphila bogotensis*; **b** *Baccharis latifolia*; **c** *Boehmeria aspera*; **d** *Clusia multiflora*; **e** *Gynoxys* spp.;

**f** *Hedyosmum luteynii*; **g** *Miconia* spp.; and **h** *Podocarpus glomeratus*. Shapes correspond to scenarios. Values presented are means for three repeated simulations for reforestation onset in 2010. Note that the y-axis values are not fixed

increases the probability of extinction (Ellstrand and Elam 1993; Fischer and Lindenmayer 2007). Harrison (1999) found a higher local endemic plant diversity ( $\alpha$ -diversity) and among-site differentiation ( $\beta$ -diversity)

on small patches when comparing communities from patchy and continuous habitats. In Yucatan Peninsula in Mexico, larger regenerating forest patches with fewer edges had higher woody species diversity

compared to small regenerating forest patches of irregular shapes (Hernández-Stefanoni et al. 2011). Arroyo-Rodríguez et al. (2009) found that patch size explained density-area relationships of plants in highly fragmented landscapes. However, richness of native and non-native plants did not increase with size of planted revegetation established on agricultural land in Gippsland southeastern Australia (Munro et al. 2009), which might be the result of insufficient maturity to display significant species density-area relationships.

Fragmentation in human-modified landscapes leads to the decrease in mean patch size and thus the creation of more forest edges (Fischer and Lindenmayer 2007). Several studies have suggested that light-demanding generalist, exotic, and invasive species may benefit from edge environments in tropical forest remnants (Harper et al. 2005; Tabarelli et al. 2010). Natural regenerating forests that persist as isolated small patches were recognized as edge-affected habitats (Tabarelli et al. 2012) and represented a suitable habitat for a subset of species only (Barlow et al. 2007). The absence of species-area relationships in the LANDIS-II model could explain the lack of patch size effect during model simulations. Nonetheless, empirical work demonstrates the importance of patch size for species conservation (Arroyo-Rodríguez et al. 2009; Hernández-Stefanoni et al. 2011).

#### Species restoration over time

As found by other studies, age structure of regenerating fallows was an important determinant for biodiversity recovery (Guariguata and Ostertag 2001; Barlow et al. 2007; Dent and Wright 2009; Norden et al. 2009). In a quantitative review of the value of natural regenerating forests across the tropic, it was found that similarity to old-growth forests increased rapidly with age (Dent and Wright 2009). Interestingly, we found a decrease in species richness over time for all scenarios, due to the decline of short-lived, shade-intolerant pioneer species several years after colonization. This process indicates a shift in successional stages of reforestation, with shade-intolerant, short-lived pioneers being replaced by long-lived pioneers and generalist species (Wirth et al. 2009). Long-term species time-series data are rare for tropical forest sites (Gardner et al. 2009). As a consequence, recolonization trajectories over longer

time periods are not well understood. In temperate forests, however, the decline in species richness as forest succession shifts to later stages is well recorded (e.g., Horn 1974; Vetaas 1997; Bonet and Pausas 2004; Amici et al. 2013).

#### Species restoration and altitude

In the Andes, altitude is an important factor that affects plant community composition (Young 1993; Lauer and Rafiqpoor 2000), which supports our findings. Variations in species composition related to altitude were most obvious in disturbed forest fragments and played a role in recolonization of regenerating pastures (MacLaren et al. 2014). It has been suggested that the creation of more open areas at high altitudes in the Andes, due to agriculture and pasture expansion, benefits the establishment of woody species associated with tree line, alpine shrub land, or páramo (Sarmiento 2002; MacLaren et al. 2014). Consistent with our findings, regenerating pastures in highland areas may prove beneficial for woody species associated with high altitudes in lower regions previously covered with mature forest. This phenomenon is thought to be widespread in the Andes (Sarmiento 2002). Nevertheless, the establishment of small pioneer shrub or tree species, such as *B. latifolia*, promoted the regrowth of other sensitive species (Posada et al. 2000). At very high altitudes (>3400 masl), growth of woody species lagged behind due to lower temperatures causing trees to grow slowly (Rapp et al. 2012). Natural regeneration of abandoned fallows is therefore limited at high altitudes.

#### Species restoration in planted forests

Our simulations showed that planted pine forests provided no benefits for biodiversity recovery. Nonetheless, almost all forest plantation activities in Ecuador have involved the planting of exotic species, such as *Pinus* and *Eucalyptus* spp. In regions with a high endemic biodiversity, such as the highlands of Ecuador, exotic plantations posed a high risk to native vegetation (Bremer and Farley 2010) and altered hydrological properties of soils (Farley et al. 2004; Molina et al. 2012). Plantations may provide habitats for certain species and increase forest connectivity if managed with long rotations and if located around natural forest fragments (Meyfroidt and Lambin 2011).

Lindenmayer et al. (2009) found that compositional heterogeneity at the landscape scale partly determines the level of biodiversity supported by plantation landscapes. Bird species richness was significantly reduced by 4–9 species in patches of native eucalypt forest where surrounding stands of exotic *Pinus radiata* were clear-felled compared to patches where surrounding pine stands remained unlogged (Lindenmayer et al. 2009). However, spatial heterogeneity was not accounted for in our plantation scenario and may affect species recovery at the landscape scale.

### Limitations

Forest landscape models explicitly represent spatial processes such as seed dispersal and disturbance spread. The value of forest models does not lie in the exact prediction of future conditions, but in their potential to explore the consequences of explicitly stated assumptions. They allow for considerable experimentation with different landscape patterns and human processes that would not be possible in the field given time and money constraints. Nevertheless, the dependence on relationships estimated in the past to predict future dynamics is a limitation to all forest models (Gustafson 2013), which makes it difficult to perform rigorous model validation. In the tropics, there is a lack of long-term data on the ecological behavior of forests, which hinders model parameterization. The greatest uncertainties for model parameterization in this study were: (i) the dispersal ability of modeled species; (ii) establishment probabilities of tree species across the landscape; and (iii) initial forest composition and age structure. We addressed these uncertainties by including high resolution remote sensing imagery, MaxEnt models, scientific literature, and consultations of local experts.

Some other factors that potentially affect future species distribution were not taken into account, such as climate change, differences in microhabitat, and seed dispersal. Andean plant species are predicted to shift their distributions to higher altitudes in response to changes in temperature and humidity (Feeley and Silman 2010). Microhabitat differences in soil fertility can also strongly affect competition and growth during re-colonization (Guariguata and Ostertag 2001). Additionally, animal movement is influenced by landscape patterns and affects seed rain (Jesus et al. 2012). We neglected the presence of seed banks from which seeds

of mostly shrubs and short-lived pioneer trees may establish at the time of abandonment during natural regeneration (Holl 2007). Finally, in the Ecuadorian Andes, many farmers leave remnant trees and shrubs on agricultural lands and, in some cases, allow vegetation to regenerate (Middendorp, *pers. obs.*). Our assumption that cultivated lands were bare may have underestimated the natural regeneration potential during model simulations.

### Conclusion and policy recommendations

Forest regeneration might prove fundamental to future conservation initiatives, but the value of regenerating forests is context dependent. Conservation policies have started to recognize the role of forest regrowth at the landscape level (Harvey et al. 2008). Reducing deforestation and increasing forest cover became a national priority under the Ecuadorian National Development Plan, known as the Plan for Good Living 2009–2013. For example, reforestation plans will be incorporated in the SocioBosque program, in which the Ministry of Environment (MAE) offers yearly monetary payments to private and communal landholders in return for maintaining forest cover (de Koning et al. 2011). A better integration of restoration ecology and landscape ecology is needed for mainstreaming successful programs (Metzger and Brancalio 2013). Our research provides specific guidelines for the design of reforestation projects that enhance biodiversity restoration in human-modified landscapes. Spatial targeting of reforestation should take into account the presence of natural remnant forest patches, the spatial pattern of the landscape, altitudinal gradients, and the type of regenerating forest, as summarized below.

We emphasize that the conservation and regeneration of natural remnant forest patches is crucial. A considerable fraction of human-modified landscapes no longer serves as a source of seed dispersal due to habitat loss. This may impose a limitation for natural forest regeneration (Zimmerman et al. 2000). The proximity and cover percentage of surrounding remnant forest patches is an important factor that determines the success of natural regeneration after abandonment. Subsequent management and conservation of regenerating forests is essential, because regenerating forests need to reach a certain age to become a source of propagules (van Breugel et al. 2013).

Additionally, we suggest that diversity and spatial arrangement of habitat patches determines the successful recolonization of the species that inhabit different environmental conditions. Based on our research, we recommend maintaining compositional heterogeneity as an important guideline in conservation management. Even though our results did not show a significant effect of patch size on species restoration, we recommend stimulating the regeneration of large and aggregated patches of natural regenerating forests. Habitat-specialists that need large areas of contiguous habitat for their survival may disappear from landscapes with high fragmentation and compositional heterogeneity (Fahrig et al. 2011). The limitations of conservation efforts to small forest fragments only risks biotic homogenization of forest-requiring species, as shown in the northern parts of the Atlantic Forest region in Brazil (Lôbo et al. 2011).

Natural regeneration following fallow abandonment often occurs on marginal lands (Crk et al. 2009), such as upland areas (Asner et al. 2009). Our results suggest, however, that reforestation in upland areas might not be enough for species recovery. We recommend that natural regeneration be encouraged at various altitudes, allowing a variety of species associated with different elevation ranges to recover at the landscape scale.

Finally, we found that planted forests using exotic pine species provided no benefits for species recovery. Active planting of native species might stimulate restoration of native biodiversity, especially in regions where natural land covers are strongly diminished.

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