

# Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar

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**Abstract** Slash-and-burn agriculture is an important driver of deforestation and ecosystem degradation, with large effects on biodiversity and carbon sequestration. This study was conducted in a forest in Madagascar, which consists of fragments of slash-and-burn patches, within a matrix of secondary and primary forest. By recording species richness, abundance, and composition of trees, shrubs, and herbs in fallows of various age and slash-and-burn history, and in the secondary and primary forest, we show how slash-and-burn intensity (number of cycles, duration of abandonment), years since last abandonment, and environmental factors (distance to primary forest and topography) affect the natural succession and recovery of the forest ecosystem. We used ordination analyses to examine how the species composition varied between the different successions stages, and to examine tree recruitment. Our results show shrub dominance the first years after abandonment. Thereafter, a subsequent increase in species richness and abundance of tree seedlings and saplings suggests a succession towards the diversity and composition of the secondary and primary forest, although a big gap between the oldest fallows and the secondary forest shows that this will take much more than 30 years. A high number and frequency of slash-and-burn cycles decreased tree seedling and sapling richness and abundance, suggesting that reducing slash-and-burn intensity will increase the speed of tree recruitment and fallow recovery. Trees can be planted into fallows to speed up vegetation and soil recovery, such that fallows can be usable within needed time and thus the extension of cultivated areas reduced. We recommend further testing of six potential species for restoration based on their early colonization of the fallows and their survival through vegetation succession.

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## Introduction

The global loss of forested areas is considered one of the largest threat to humanity, not only due to the loss of biodiversity in forests, but also due to the reduced amount of sequestered carbon (Houghton et al. 2000; Grace 2004). Slash-and-burn agriculture is one of the main drivers of deforestation and subsequent land degradation, and is currently practiced by ca. 300–500 million people to provide food and an occasional small amount of income from cash crops (Brady 1996). Slash-and-burn agriculture initially involves the cutting of forest followed by burning of the plant material. Thereafter slashed and burned areas are subjected to a cycle of cultivation and abandonment. The duration of each cycle period depends on factors such as soil fertility, the crop type, the availability of crop areas, and population growth (Smith et al. 1999; Styger et al. 2007). Due to the low nutrient content of tropical soils, slash-and-burn, like other farming systems not using fertilizer, is a low-yield agriculture system. Coupled with increased human population size, particularly in the tropics, that cause increased demands of food, people are broadly left with two options. Either they start to use fallow areas after a shorter period of soil recovery (during which nutrient content builds up) (Dalle and de Blois 2006), or they extend the area of cultivation into primary or secondary forests (Gehring et al. 2005; Styger et al. 2007). At both global and local levels, this results in a loss of forested areas, causing decreased amounts of sequestered carbon that could mitigate anthropogenic emissions of CO<sub>2</sub> (Houghton et al. 2000) and result in a potential loss of biodiversity (e.g. Sala et al. 2000).

In Madagascar, containing unique, and one of the richest floras and faunas of the world (Myers et al. 2000), slash-and-burn agriculture has been attributed the main cause of primary forest fragmentation and loss, and soil degradation, during the last 150 years (e.g. Oxby and Boerboom 1985; Gade 1996; Marcus 2001). In Madagascar, as elsewhere, fallow periods are shortened, primarily due to lack of, or not readily adopted, alternative incomes and food types, and because of increased population growth (Styger et al. 2007). Both nationally (Madagascar Action Plan 2007–2012) and internationally (e.g. Green and Sussman 1990; Myers et al. 2000) there is a growing concern about the accelerating loss of forests in Madagascar, and knowledge that could contribute to reduce or stop primary forest loss and halt further fragmentation of existing forest areas is apparently still needed.

In this work, we study the effects of slash-and-burn agriculture on plant species richness, abundance, and composition, and the natural succession and recovery of plant communities after disturbance. Our study was conducted in the Vohimana forest fragment, situated between the three larger primary evergreen forests Mantadia National Park, Analamazaotra, and Maromizaha, towards the eastern coast of Madagascar. The position of the Vohimana forest, as a small isolated forest patch between the larger forests, is potentially important for forming a forest corridor that could connect these larger primary forest areas. Man and the environment (MATE <http://www.madagascar-environnement.com/>) has been involved in the conservation of Vohimana since 2003, and several studies have documented large negative effects of slash-and-burn agriculture on the faunistic and floristic diversity in the area (e.g. Rabemananjara et al. 2003; Randrianirina 2005). Vegetation succession after abandonment of slash-and-burn areas has also been studied in other areas of Madagascar (Lowry et al. 1997; Styger et al. 2007), South America (e.g. Uhl

1987; Miller and Kauffman 1998; Smith et al. 1999; Gehring et al. 2005), and in South East Asia (e.g. Roder et al. 1997). However, little knowledge exists on how variation in slash-and-burn intensity and the colonisation of primary and secondary forest species into fallows, affect the speed and direction of natural succession and the recovery of the forest ecosystem (but see Guariguata and Ostertag 2001; Dalle and Bois 2006; Styger et al. 2007). Slash-and-burn agriculture can be seen as a series of disturbances, where each stage (cutting, burning, weeding) have dramatic effects on the mortality and regeneration of plant species (Uhl 1987). Moreover, the combined effect of each of these stages may reduce or eliminate the potential for on-site tree regeneration, leaving seed dispersal as the major way for establishment of species from the nearby primary forest. A key factor of fallow succession is the re-establishment of forest species, which can be a slow process (e.g. Uhl 1987; Guariguata and Ostertag 2001; Brearley et al. 2004), although some species, in particular those adapted to colonizing forest gaps, may establish fast. Studies have shown that planting of trees, or single remnant trees, such as for example fruit trees, and logs, may facilitate tree regeneration through shading of the seedlings (Uhl 1987) or by nucleation due to the attraction of seed dispersers (Guariguata and Ostertag 2001; Carrière et al. 2002). On the other hand, dense canopies of pioneer shrubs that invade fallows are predicted to inhibit the growth of tree seedlings (Styger et al. 2007), although this may be species dependent, as some may even facilitate the establishment of trees. Indeed, more knowledge is needed to understand the relationship between early colonizers and fallow succession. By obtaining detailed information on the intensity of use (number of slash-and-burn cycles and average fallow duration), time since last abandonment of slash-and-burn fallows, and the species richness and composition of fallows and secondary and primary forest, we aim to answer the following questions: (1) how do species richness and the abundance of trees (seedlings, saplings, adults), shrubs, and herbs develop after abandonment of slash-and-burn areas, (2) how does slash-and-burn intensity affect vegetation succession and recovery of fallows, (3) how do distance to the primary forest, altitude, and slope affect the vegetation succession and recovery of fallows, and (4) based on our results; which local species may be suitable candidates in an active restoration programme of the degraded forest areas in the study area?

## Materials and methods

### Study area

Vohimana forest (18°54′–18°56′S, 48°28′–48°31′E) is situated at ca. 700–1000 m elevation ca. 150 km east of Antananarivo, Madagascar's capital city, and ca. 6 km north of the village Ambavaniasy. The climate is hot and humid, highly influenced by moist winds from the east, and with no dry season. Average annual precipitation is 1850 mm and average annual temperature is 20.4°C. The Vohimana area consists of a patchwork of fallows of various ages in a matrix of secondary and primary forest patches of different sizes. The natural forest is a wet and dense evergreen forest (Randrianirina 2005). Areas below ca 800 m altitude belong to the floristic zone characterized by *Anthostema* and *Myristicaceae* tree species, whereas areas above ca 800 m altitude are characterised by *Weinmannia* and *Tambourissa* tree species (Faramalala and Rajeriarison 1999). What we define as secondary forest in this study is an intact forest disturbed by selective harvesting, tree cutting and/or uncontrolled fire. The fallows are dominated by herbs (e.g. *Asteraceae*, *Poaceae*) and shrubs (e.g. the native *Psiadia altissima* and the introduced invasives

*Lantana camara* and *Rubus mollucanus*) and have only a few single trees (the introduced *Trema orientalis* and the native *Croton mongue*).

## Field methods

We selected 33 slash-and-burn areas where we had reliable information on the start of the slash-and-burn period, the number of slash-and-burn cycles, and the number of years since the last abandonment. This information was obtained by interviewing people using the area and a local guide. Our sample of fallows represents the current variation of fallow duration in the Vohimana area, with the oldest plots started being used for slash-and-burn in 1930, and with a range from 1 to 26 years since the last exploitation. In addition, we randomly selected 12 plots in secondary and 6 in primary forest in order to compare species richness, abundance, and composition in fallows with that of secondary and primary forest plots. In fallows and secondary forest,  $5 \times 30$  m plots were positioned in the centre of the fallow or forest patch. Each plot consisted of six  $5 \times 5$  m sub-plots and each sub-plot had a  $1 \times 1$  m quadrat in its centre. We measured the diameter at breast height of each plant taller than 1.3 m (dbh) at 1.3 m height with a dbh-meter. For trees and shrubs with a dbh of  $>10$  cm, we counted the individuals of all species within each of the six sub-plots. Individuals with  $\text{dbh} < 10$  cm and height  $>1$  m were counted and determined as far as possible to species or genus in every second sub-plot. We estimated the abundance of all plants  $<1$  m by recording the percentage cover within each of the  $1 \times 1$  m quadrats. Trees with  $\text{dbh} > 10$  cm were defined as adults, trees with  $\text{dbh} < 10$  cm and height  $>1.3$  m were defined as saplings, and trees  $<1.3$  m height were defined as seedlings. In the primary forest we used  $15 \times 30$  m plots, divided into three  $5 \times 30$  m plots and 18 sub-plots to estimate species richness, abundance, and composition. We used a larger plot size here in order to capture the variation in the tree species composition. Apart from the difference in plot size, the methodology of obtaining data on the presence and abundance of species in the primary forest was as described above. To correct for the three times larger plot size in the primary forest, species counts (abundance) for each large plot were divided by three before data analyses. For species richness, we calculated the number of species for each of the three  $5 \times 30$  m plots separately and used the mean. Plots in the primary forest were positioned at least 100 m away from the forest edge towards fallow or secondary forests to avoid any edge effects. For each plot in fallows we estimated the distance to the closest part of the primary forest. For all plots, we measured the altitude and the coordinates with a GPS, the slope with a clinometer, and the exposition with a compass.

## Statistical analyses

The fallows were divided into 4 age categories, depending on the number of years since the last abandonment (1: 1–3 years; 2: 4–7 years; 3: 8–12 years; 4: 13–26 years). Secondary and primary forests were set as age class 5 and 6, respectively. We used one-way ANOVAs to examine if total species richness (all species), and species richness and abundance of herbs, shrubs, tree seedlings, tree saplings, and adult trees (dependent variables) differed among age classes (fixed variable). We used the Tukey's HSD post-hoc test to examine if response variables differed significantly between individual age classes.

Due to the Poisson distributions observed in the dependent variables in the fallows, we used Generalized Linear Model multiple regressions with a log link function to examine the relative importance of the different environmental variables for species richness and

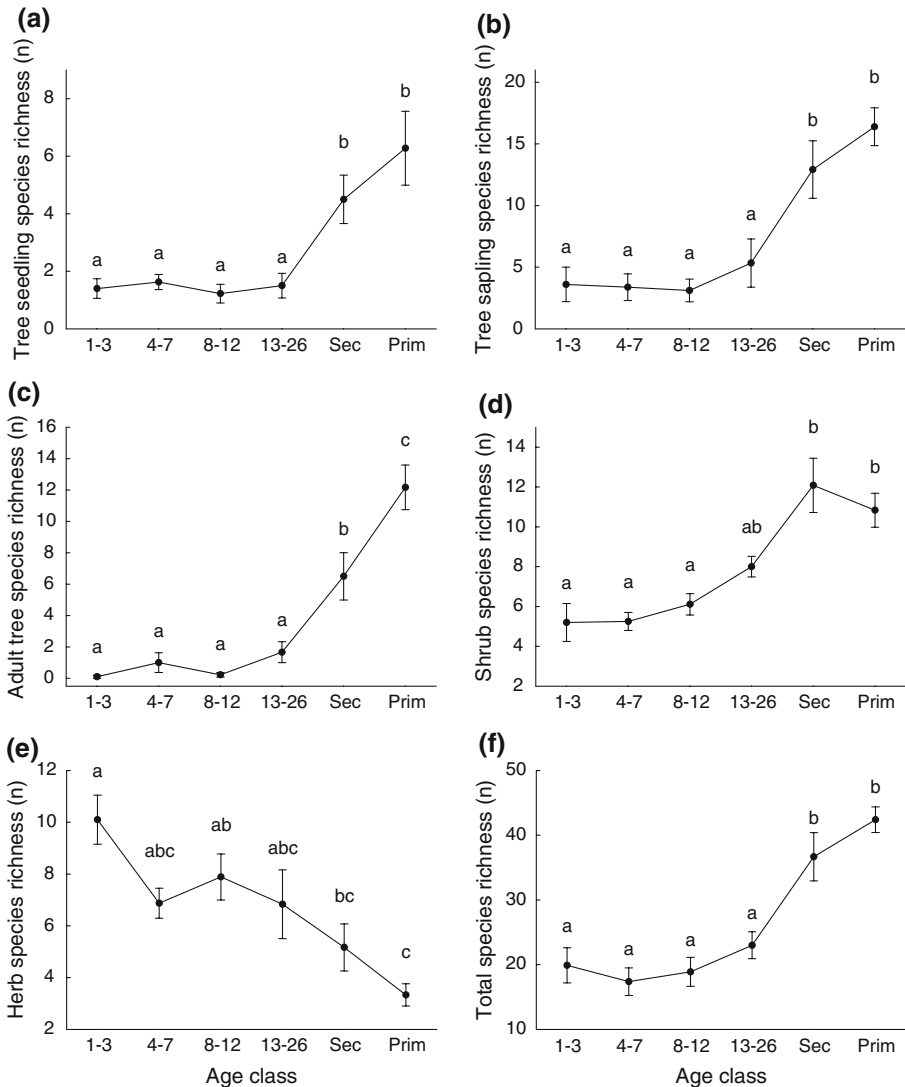
abundances there. The environmental variables used were (a) linear distance from the fallow to the primary forest, (b) slope of the fallow, (c) years since last abandonment of the fallow, (d) the number of slash and burn cycles of the fallow, and (e) the slash and burn intensity, measured as the number of years from the first slash and burn event to last abandonment divided by the number of slash and burn cycles. Altitude and total duration of the cultivation period were not included in the regressions due to high collinearity with other variables. We used SYSTAT (version 10 for Windows) for the ANOVAs and Statistica (Version 8) for the Generalized Linear Models.

We used multivariate ordination analyses to examine how species composition of herbs, shrubs, tree seedlings, saplings, and adults varied among fallows and the secondary and primary forests. Furthermore, we used another set of multivariate analyses in the fallows only to assess how the measured environmental variables contributed to explaining the variation in species composition among fallows. In order to identify species potentially useful for restoration based on natural recruitment and survival, we used the results of the analyses above to examine the relationship between individual species, fallow or forest succession stage, and environmental variables. Because the abundance of tree seedlings and shrubs was estimated both as percentage cover and counts, depending on plant size, we used presence/absence data of these groups in the analyses. Abundance data of all other groups of species are counts. Detrended correspondence analysis (DCA) was used to examine the gradient length in the tree seedling, sapling, adult, shrub, and herb data separately. Because of a relatively large gradient length for all the groups (total variation  $>2.0$  SD in all cases), we chose to use canonical correspondence analysis (CCA) to assess the relationships between the environmental variables and species composition. CCA constrained by age class as an environmental variable was used to test if there were significant differences in species composition among age classes. For the fallows, we tested each of the environmental variables by forward selection with all variables included and with 999 unrestricted permutations in a Monte Carlo test. Only significant ( $P < 0.05$ ) variables were included in the final model. All ordinations were computed by default settings in CANOCO 4.5, and graphs produced in CanoDraw (Ter Brak and Smilauer 2002).

## Results

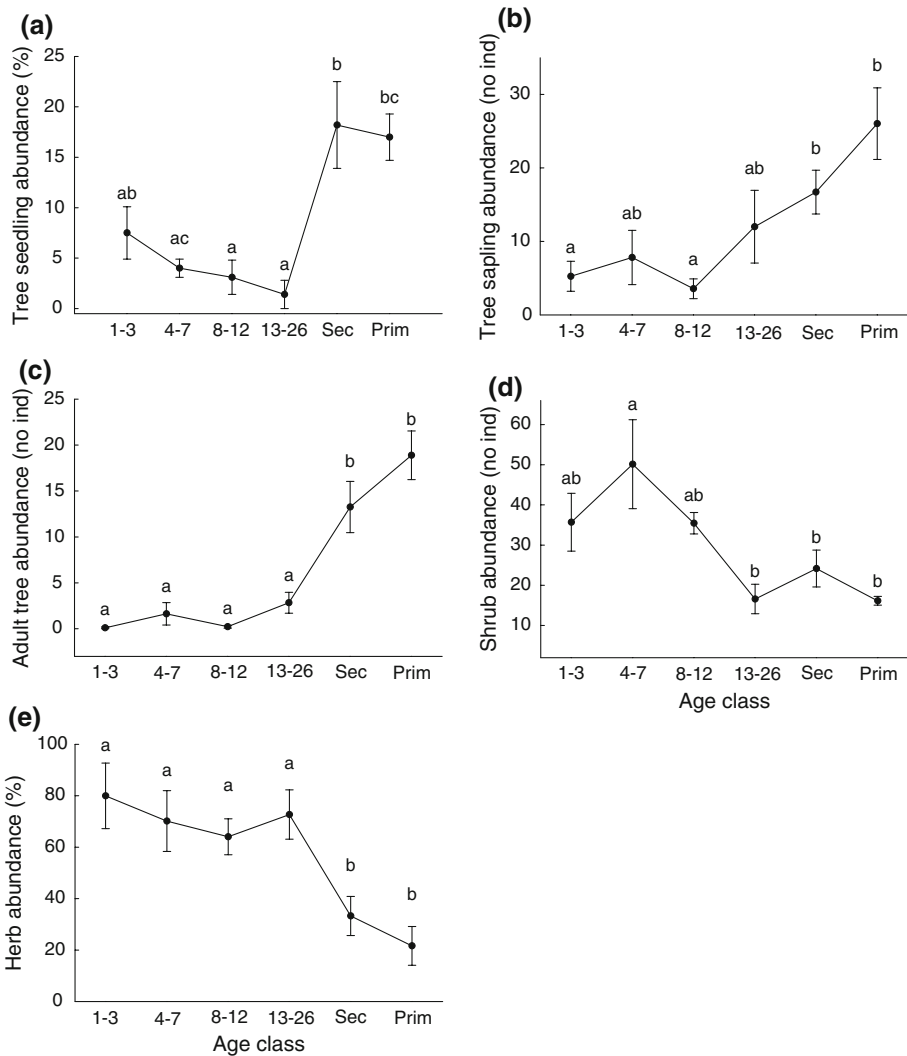
### Species richness and abundance

One-way ANOVAs showed that the species richness of tree seedlings ( $F_{5,45} = 9.02$ ,  $P < 0.001$ ), saplings ( $F_{5,45} = 9.81$ ,  $P < 0.001$ ), and adults ( $F_{5,45} = 18.94$ ,  $P < 0.001$ ) all increased from the fallows to the secondary and primary forest, but Tukey's test showed that species richness did not differ among fallows of various age for any group (Fig. 1a–c). Tree seedling and sapling species richness did not differ significantly between secondary and primary forest (Fig. 1a, b), whereas species richness of adult trees was significantly higher in the primary than in the secondary forest (Fig. 1c). Species richness of shrubs did not differ among fallows, but was significantly higher in the secondary and primary forest ( $F_{5,45} = 9.70$ ,  $P < 0.001$ ; Fig. 1d). Species richness of herbs decreased gradually from the youngest fallows to the secondary and primary forest ( $F_{5,45} = 6.20$ ,  $P < 0.001$ ; Fig. 1e). Total species richness increased from the fallows to the secondary and primary forest ( $F_{5,45} = 15.83$ ,  $P < 0.0001$ ) with no differences among fallows or between secondary and primary forest (Fig. 1f).



**Fig. 1** Species richness of tree seedlings (a), saplings (b), adults (c), shrubs (d), herbs (e), and total species richness (f) in fallows of different age classes and secondary (Sec) and primary (Prim) forest in Vohimana forest, Madagascar. Error bars are standard error. Bars not sharing a letter differ significantly (Tukey's hsd,  $P < 0.05$ )

The abundance of tree seedlings increased significantly from the oldest fallows to the secondary and primary forest ( $F_{5,45} = 5.87$ ,  $P < 0.001$ ), with significant differences between the three oldest fallow age-classes and the secondary forest, and between the two oldest fallow age-classes and the primary forest (Fig. 2a). Tree saplings ( $F_{5,45} = 5.65$ ,  $P < 0.001$ ) and adults ( $F_{5,45} = 19.89$ ,  $P < 0.001$ ) increased in abundance from the youngest fallows to the secondary and primary forest, with no differences between fallows age-classes or between the secondary and primary forests (Fig. 2b, c). The abundance of shrubs, on the other hand, decreased from the youngest fallows to the primary forest



**Fig. 2** Species abundances of tree seedlings (a), saplings (b), adults (c), shrubs (d), and herbs (e) in fallows of different age classes (1–4), secondary (5), and primary forest (6) in the Vohimana forest, Madagascar. Tree seedlings and herbs are measured as % cover, whereas all other groups are number of stems. Error bars are standard error. Bars not sharing a letter differ significantly (Tukey’s hsd,  $P < 0.05$ )

( $F_{5,45} = 4.18, P = 0.003$ ), with a significant difference between the second age class where shrub abundance peaked, and the older fallows, and secondary and primary forest (Fig. 2d). Herb abundance decreased from the fallows to the secondary and primary forest ( $F_{5,45} = 6.66, P < 0.001$ ), with no difference among fallow age-classes or between the two forests types (Fig. 2e).

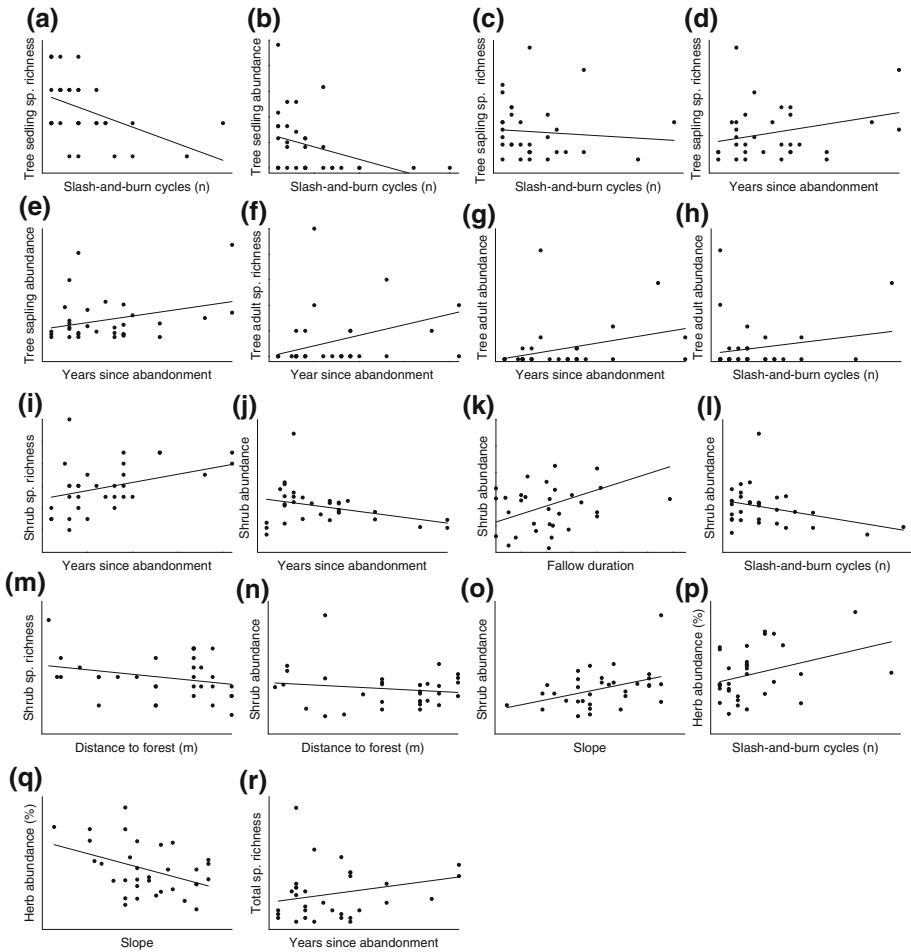
Generalized Linear Models multiple regressions showed that species richness and abundance of tree seedlings, and richness of saplings, decreased with increasing number of slash-and-burn cycles imposed to the fallows (Table 1; Fig. 3a–c). No other variables were significantly related to seedling species richness or abundance (Table 1). The richness and

**Table 1** Generalized Linear Model multiple regressions with a log link function of the relationships between fallow parameters (predictors) and the species richness and abundances of tree seedlings, saplings, adults, shrubs, herbs, and all species recorded in the fallows in Vohimana forest, Madagascar

| Predictors                | Tree seedlings |              | Tree saplings |              | Tree adults |                | Shrubs      |                | Herbs        |              | All species |              |
|---------------------------|----------------|--------------|---------------|--------------|-------------|----------------|-------------|----------------|--------------|--------------|-------------|--------------|
|                           | Est.           | P            | Est.          | P            | Est.        | P              | Est.        | P              | Est.         | P            | Est.        | P            |
| <b>Species richness</b>   |                |              |               |              |             |                |             |                |              |              |             |              |
| Distance to forest        | -0.00          | 0.145        | -0.00         | 0.916        | 0.00        | 0.185          | -0.00       | <b>0.035</b>   | -0.00        | 0.446        | -0.00       | 0.969        |
| Years since abandonment   | 0.00           | 0.846        | <b>0.04</b>   | <b>0.013</b> | <b>0.10</b> | < <b>0.001</b> | <b>0.02</b> | <b>0.015</b>   | -0.02        | 0.213        | <b>0.02</b> | <b>0.010</b> |
| Slash and burn cycles (n) | <b>-0.10</b>   | <b>0.007</b> | <b>-0.06</b>  | <b>0.047</b> | -0.04       | 0.445          | -0.02       | 0.228          | -0.01        | 0.213        | -0.02       | 0.203        |
| Fallow duration           | 0.00           | 0.925        | -0.07         | 0.063        | -0.19       | 0.098          | 0.01        | 0.548          | 0.02         | 0.285        | -0.00       | 0.810        |
| Slope                     | 0.00           | 0.943        | 0.00          | 0.748        | -0.01       | 0.361          | -0.01       | 0.229          | -0.00        | 0.836        | 0.00        | 0.818        |
| <b>Species abundances</b> |                |              |               |              |             |                |             |                |              |              |             |              |
| Distance to forest        | -0.00          | 0.288        | -0.00         | 0.230        | 0.00        | 0.752          | -0.00       | <b>0.019</b>   | 0.00         | 0.270        |             |              |
| Years since abandonment   | -0.12          | 0.130        | <b>0.06</b>   | <b>0.038</b> | <b>0.13</b> | < <b>0.001</b> | -0.93       | <b>0.046</b>   | -0.01        | 0.465        |             |              |
| Slash and burn cycles (n) | <b>-0.39</b>   | <b>0.010</b> | -0.04         | 0.389        | <b>0.06</b> | <b>0.040</b>   | -1.35       | <b>0.036</b>   | <b>0.02</b>  | <b>0.051</b> |             |              |
| Fallow duration           | -0.06          | 0.524        | -0.03         | 0.628        | -0.20       | 0.152          | <b>3.04</b> | < <b>0.001</b> | 0.00         | 0.773        |             |              |
| Slope                     | -0.03          | 0.055        | 0.01          | 0.662        | 0.00        | 0.844          | <b>0.53</b> | <b>0.001</b>   | <b>-0.01</b> | <b>0.018</b> |             |              |

Predictor variables, parameter estimates (Est.) and P-values are shown for each model, significant values ( $P < 0.05$ ) are in bold. Goodness of fit (statistics/d.f.)  $\approx 1$  in all cases





**Fig. 3** Relationships between species richness and abundances of tree seedlings, saplings, adults, shrubs, herbs, and all species recorded in the fallows in Vohimana forest, and significant ( $P < 0.05$ ) fallow parameters in GLM multiple regressions. See Table 1 for regression results

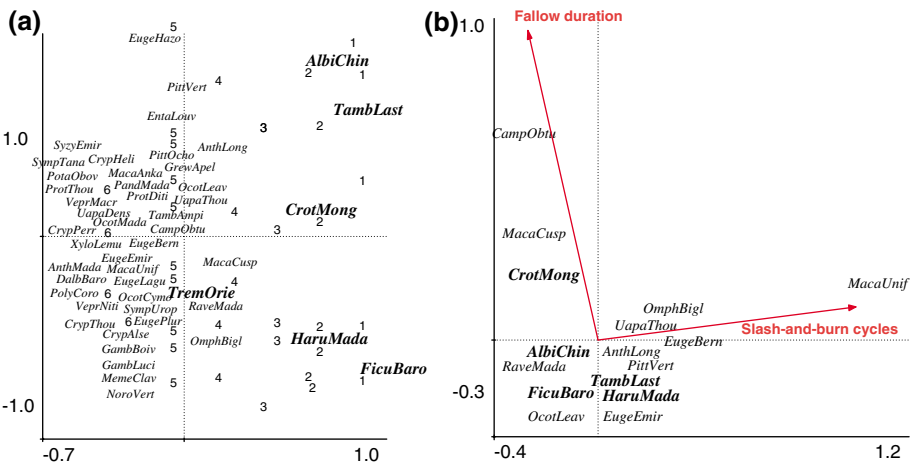
abundance of tree saplings and adults increased with the number of years since abandonment (Table 1; Fig. 3d–g), whereas the abundance of adult trees was positively related to the number of slash-and-burn cycles (Table 1; Fig. 3h). Shrub species richness also increased with years since abandonment, whereas shrub abundance slightly decreased (Table 1; Fig. 3i, j). Shrub abundance was most strongly related to cultivation intensity, and increased with fallow duration and decreased with number of slash-and-burn cycles (Table 1; Fig. 3k, l). Both species richness and abundance of shrubs decreased with the distance to the primary forest (Table 1; Fig. 3m, n), and shrub abundance increased with the steepness of the fallow slopes (Table 1; Fig. 3o). There were no significant relationships between herb species richness and any of the fallow parameters, whereas herb abundance increased with the number of slash-and-burn cycles and decreased with the steepness of the slope (Table 1; Fig. 3p, q). Total species richness increased with the number of years since abandonment (Table 1; Fig. 3r).

Species composition

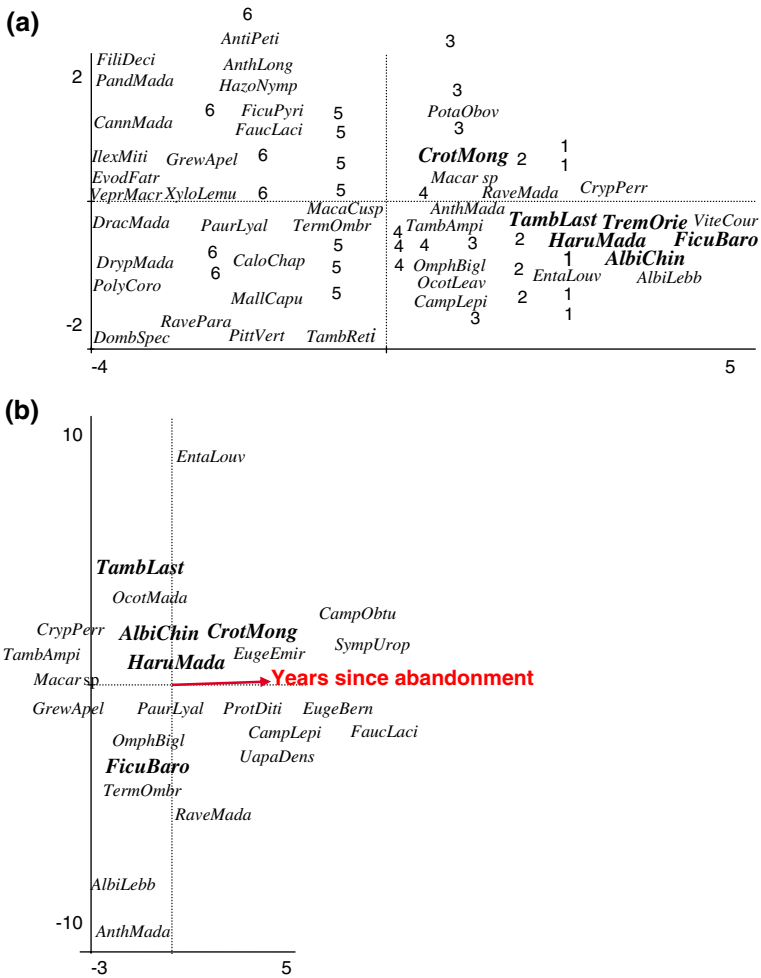
Canonical correspondence analysis (CCA) showed that tree seedling species composition changed significantly from the youngest fallows to the secondary and primary forest ( $F = 2.35, P = 0.001$ ; Fig. 4a). In the fallows, forward selection of the environmental variables showed that the total number of slash-and-burn cycles ( $F = 2.37, P = 0.002$ ) and fallow duration ( $F = 1.74, P = 0.086$ ) were the variables most related to the tree seedling species composition (Fig. 4b). Species composition of tree saplings also changed significantly from fallows to primary forest ( $F = 2.59, P = 0.001$ ; Fig. 5a). Forward selection showed that the number of years since abandonment was significantly related to tree sapling species composition in the fallows ( $F = 1.74, P = 0.039$ ; Fig. 5b). There was no significant relationship between the species composition of tree seedlings or saplings and any of the other environmental variables ( $F < 1.19, P > 0.237$  in all cases). There was no significant change in the species composition of adult trees from the youngest fallow to the primary forest ( $F = 1.18, P = 0.172$ ; Fig. 6a). In fallows, the species composition of adult trees was significantly related to the number of slash-and-burn cycles ( $F = 1.04, P = 0.014$ ; Fig. 6b). Shrub species composition changed with the number of years since abandonment, as shown in Fig. 7a ( $F = 5.37, P = 0.002$ ). Forward selection of the environmental variables showed that shrub species composition in the fallows were significantly related to the number of years since abandonment ( $F = 3.76, P = 0.002$ ) and the number of slash-and-burn cycles ( $F = 2.18, P = 0.034$ ), although the two most abundant species in the fallows (*Psiadia altissima* and *Lantana camara*) appeared to be independent of any of the environmental variables (Fig. 7b).

Potential species for restoration

The CCAs showed that some tree seedling species (*Albizia chinensis*, *Croton mongue*, *Ficus baronii*, *Harungana madagascarensis*, *Tambourissa lastelliana*) were associated

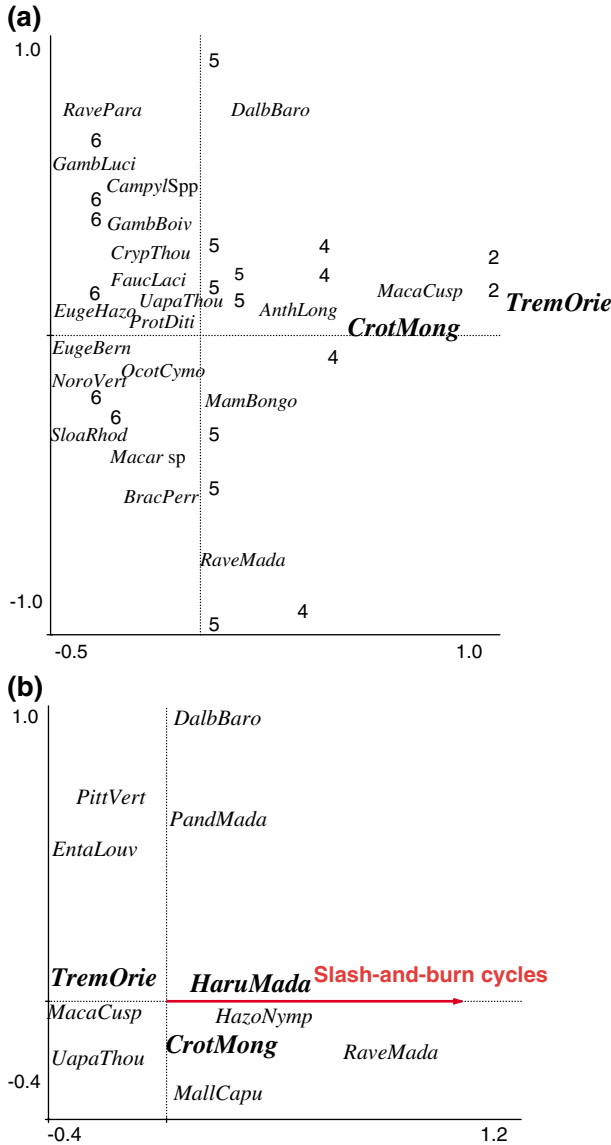


**Fig. 4** a CCA attribute plot of tree seedling species composition from the youngest fallows (1–4) to the secondary (5) and primary forest (6), and b CCA biplot of tree seedling species composition and environmental variables selected by the forwards selection procedure in fallows in Vohimana forest, Madagascar. Full species names are shown in Table 2



**Fig. 5** **a** CCA attribute plot of tree sapling species composition from the youngest fallows (1–4) to the secondary (5) and primary forest (6) (species >5% fit are shown), and **b** CCA biplot of tree sapling species composition and environmental variables selected by the forwards selection procedure in fallows in Vohimana forest, Madagascar. Full species names are shown in Table 2

with the youngest fallows (Fig. 4a), suggesting that these establish rapidly after abandonment. The presence of most of these species appeared to be independent of the environmental factors, i.e. they occurred close to the centre of the biplot, suggesting that they are little affected by the total number of slash-and-burn cycles or the number of years per cycle (Fig. 4b). Most of these species, in addition to a few others, such as *Trema orientalis*, also occurred as saplings in young fallows (Fig. 5a, b), and three of these species (*H. madagascarensis*, *C. mongue*, and *T. orientalis*) were also associated with the fallows as adults. None of the trees associated with the fallows as seedlings or saplings were associated with the secondary or primary forest as adults (Fig. 6a, b), but both *C. mongue* and *T. lastelliana* occurred in the study plots.

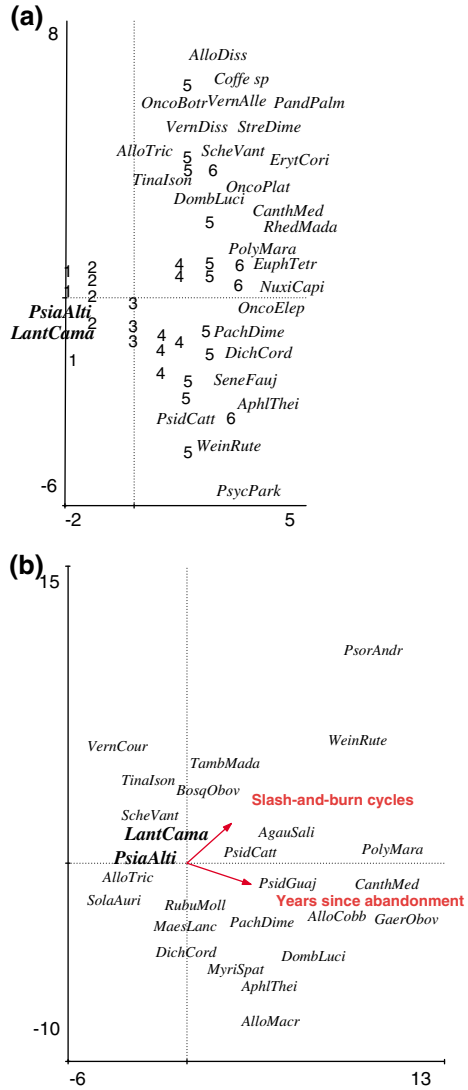


**Fig. 6** **a** CCA attribute plot of adult tree species composition from the youngest fallows (1–4) to the secondary (5) and primary forest (6) (species >5% fit are shown), and **b** CCA biplot of adult tree species composition and environmental variables selected by the forwards selection procedure in fallows in Vohimana forest, Madagascar. Full species names are shown in Table 2

**Discussion**

Slash-and-burn agriculture decreased plant species richness and affected species abundance and composition in the Vohimana forest in Madagascar to a great extent. Even after almost 30 years of abandonment, there was a big gap in total species richness, and richness and abundance of seedlings, saplings and adult trees, between the oldest fallows and the

**Fig. 7 a** CCA attribute plot of shrub species composition from the youngest fallows (1–4) to the secondary (5) and primary forest (6), species with >5% fit to the axes are shown, and **b** CCA biplot of shrub species composition and environmental variables selected by forward selection in fallows in Vohimana forest, Madagascar. Full species names are shown in Table 2



secondary and primary forest, showing that natural succession and recovery is very slow. Our results show, however, that the duration of the recovery period may be shortened by reducing the number of slash-and-burn cycles imposed to the area and the intensity of the cultivation, i.e. increasing the number of years between each slash-and-burn event.

Natural succession and recovery of degraded forest ecosystems towards intact forests depend highly on the establishment ability of tree species (Uhl 1987). One potential limitation for the establishment of tree seedlings and saplings is the extensive invasion of shrubs into open fallows (e.g. Styger et al. 2007), which may inhibit tree seedling growth and survival through competition. Our results from Vohimana show that shrubs, mainly the endemic *Psiadia altissima* and the non-native invasive *Lantana camara*, completely dominated fallows during the first years after abandonment, with a peak of ca 50

**Table 2** Full species names for abbreviations used in Figs. 4–7

| Tree species |                                      | Shrub species |                                      |
|--------------|--------------------------------------|---------------|--------------------------------------|
| AlbiChin     | <i>Albizia chinensis</i>             | AlloCobb      | <i>Allophylus cobbe</i>              |
| AlbiChin     | <i>Albizia chinensis</i>             | AlloDiss      | <i>Allophylus dissectus</i>          |
| AlbiLebb     | <i>Albizia lebbek</i>                | AlloMacr      | <i>Allophylus macrocarpus</i>        |
| AnthLong     | <i>Anthocleista longifolia</i>       | AlloTric      | <i>Allophylus trichodesmus</i>       |
| AnthMada     | <i>Anthocleista madagascariensis</i> | AphlThei      | <i>Aphloia theiformis</i>            |
| CampObtu     | <i>Campylospermum obtusifolium</i>   | BosqObov      | <i>Bosqueia obovata</i>              |
| CrotMong     | <i>Croton mongue</i>                 | Coffe sp      | <i>Coffea</i> sp                     |
| CrypPerr     | <i>Cryptocaria perrieri</i>          | DichCord      | <i>Dichaetanthera cordifolia</i>     |
| CrypThou     | <i>Cryptocaria thouvenotii</i>       | DombLuci      | <i>Dombeya lucida</i>                |
| DalbBaro     | <i>Dalbergia baroni</i>              | ErytCori      | <i>Erythoxylum corimbosum</i>        |
| EntaLouv     | <i>Entada louvelii</i>               | EuphTetr      | <i>Euphorbia tetraptera</i>          |
| EugeBern     | <i>Eugenia bernerii</i>              | GaerObov      | <i>Gaertnera obovata</i>             |
| EugeEmir     | <i>Eugenia emirimensis</i>           | LantCama      | <i>Lantana camara</i>                |
| EugeHazo     | <i>Eugenia hazompasika</i>           | MaesLanc      | <i>Maesa lanceolata</i>              |
| EugeLagu     | <i>Eugenia lagubris</i>              | MyriSpat      | <i>Myrica spathulata</i>             |
| EugePlur     | <i>Eugenia pluricymosa</i>           | NuxiCapi      | <i>Nuxia capitata</i>                |
| FicuBaro     | <i>Ficus baroni</i>                  | OncoBotr      | <i>Oncostemon botryoides</i>         |
| GambBoiv     | <i>Gambeya boiviniana</i>            | OncoElep      | <i>Oncostemon elephantipes</i>       |
| GambLuci     | <i>Gambeya lucida</i>                | OncoPlat      | <i>Oncostemon platycladum</i>        |
| GrewApel     | <i>Grewia apetala</i>                | PachDime      | <i>Pachytrophe dimepate</i>          |
| HaruMada     | <i>Harungana madagascariensis</i>    | PandPalm      | <i>Pandanus palme</i>                |
| MacaAnka     | <i>Macaranga ankafinensis</i>        | PolyMara      | <i>Polyscias maralia</i>             |
| MacaCusp     | <i>Macaranga cuspidata</i>           | PsiaAalti     | <i>Psidium altissima</i>             |
| Macar sp     | <i>Macaranga</i> sp                  | PsidCatt      | <i>Psidium cattleianum</i>           |
| MacaUnif     | <i>Macaranga unifolia</i>            | PsidGuaj      | <i>Psidium guajava</i>               |
| MemeClav     | <i>Memecylon clavistaminum</i>       | PsorAndr      | <i>Psorospermum androsaemifolium</i> |
| NoroVert     | <i>Noronhia verticillata</i>         | PsycPark      | <i>Psychotria parkeri</i>            |
| OcotCymo     | <i>Ocotea cymosa</i>                 | RhedMada      | <i>Rhedia madagascariensis</i>       |
| OcotLeav     | <i>Ocotea leavis</i>                 | RubuMoll      | <i>Rubus mollucanus</i>              |
| OcotMada     | <i>Ocotea madagascariensis</i>       | ScheVant      | <i>Schefflera vantsilana</i>         |
| OmphBigl     | <i>Omphalea biglandulosa</i>         | SeneFauj      | <i>Senecio faujasioides</i>          |
| PandMada     | <i>Pandanus madagascariensis</i>     | SolaAuri      | <i>Solanum auriculatum</i>           |
| PittOcho     | <i>Pittosporum ochosiaefolium</i>    | StreDime      | <i>Streblus dimepate</i>             |
| PittVert     | <i>Pittosporum verticulatum</i>      | TambMada      | <i>Tambourissa madagascariensis</i>  |
| PolyCoro     | <i>Polyscias colororum</i>           | TinaIson      | <i>Tina isonema</i>                  |
| PotaObov     | <i>Potameia obovata</i>              | VernAlle      | <i>Vernonia allezetei</i>            |
| ProtDiti     | <i>Protorhus ditimena</i>            | VernCour      | <i>Vernonia coursii</i>              |
| ProtThou     | <i>Protorhus thouvenotii</i>         | VernDiss      | <i>Vernonia dissoluta</i>            |
| RaveMada     | <i>Ravenala madagascariensis</i>     | WeinRute      | <i>Weinmannia rutembergii</i>        |
| SympTana     | <i>Symphonia tanalensis</i>          |               |                                      |
| SympUrop     | <i>Symphonia urophylla</i>           |               |                                      |
| SyzyEmir     | <i>Syzygium emirnense</i>            |               |                                      |
| TambLast     | <i>Tambourissa lastelliana</i>       |               |                                      |

**Table 2** continued

| Tree species | Shrub species                  |
|--------------|--------------------------------|
| TambAmpi     | <i>Tambourissa ampifolia</i>   |
| TremOri      | <i>Trema orientalis</i>        |
| UapaDens     | <i>Uapaca densifolia</i>       |
| UapaThou     | <i>Uapaca thouarsii</i>        |
| UrenLoba     | <i>Urena lobata</i>            |
| VeprMacr     | <i>Vepris macrocarpa</i>       |
| VeprNiti     | <i>Vepris nitida</i>           |
| XyloLemu     | <i>Xylopia lemurica</i>        |
| ZantThou     | <i>Zanthoxylum thouvenotii</i> |

individuals per 150 m<sup>2</sup> after 4–7 years. Then, however, shrub abundance decreased, and 13–26 years after abandonment, shrub density was at the same level as for the primary forest. Along with the decline in shrub density, species richness of shrubs and abundance of tree seedlings and saplings increased. This shows that even if shrubs dominated during the first stages of succession, tree species managed to establish at later stages. The establishment of tree seedlings, however, was more dependent on the total number of slash-and-burn cycles imposed on the fallows than the number of years since the last abandonment. This is in line with other studies showing that intensity of previous land use affect recruitment (see Guariguata and Ostertag 2001). A higher number of slash-and-burn cycles implicates more fire and soil disturbance, which subsequently remove more of the seed-bank and potentially resprouting roots and stumps (Guariguata and Ostertag 2001). The decrease in seedling species richness and abundance with increased number of slash-and-burn cycles clearly suggests that reducing the number of slash-and-burn cycles before the land is left to recover, may shorten the establishment period for new tree seedlings. This is also in line with findings of Styger et al. (2007), who showed that productivity decreased after the third slash-and-burn cycle following deforestation. To restore the soil, they suggested an increased length of fallow periods accompanied with reduced use of fire. Plants are not capable of utilizing all nutrients released by burning, resulting in nutrient loss through leaching. Furthermore, fire favours aggressive exotics over native species and herbaceous over woody species (e.g. Styger et al. 2007). The significant relationship between slash-and-burn intensity and tree seedling species composition in our ordination results suggests that both the total number of slash-and-burn cycles and the fallow duration between each slash-and-burn event have an important influence on tree seedling establishment. In contrast, the richness, abundance, and composition of tree saplings depended more on the time since abandonment than farming intensity. Thus, slash-and-burn intensity appears to be the most critical factor for the germination and growth of tree seedlings, and when the seedlings have established, the duration of the fallow period determines whether they survive as saplings.

Tree planting may be another tool to speed up the slow process of natural succession, and studies have shown that planted trees may have large effects on the recruitment of other tree species (see Guariguata and Ostertag 2001). Moreover, by selecting the most appropriate species for planting, both species richness and site quality can be restored (Guariguata and Ostertag 2001). In our study, six species were associated with the fallows as both seedlings and saplings (*Albizia chinensis*, *Croton mongue*, *Ficus baronii*,

*Harungana madagascarensis*, *Tambourissa lastelliana*, *Trema orientalis*), suggesting that these species have the ability to establish fast after the fallows are left to recover and to survive through the critical seedling phase and continue growth as saplings. Moreover, most of these species appeared to be less dependent on the degree of previous slash-and-burn activities. *Trema orientalis* and *H. madagascarensis* are both fast growing shade intolerant gap species (Schatz 2001; Styger et al. 2007), suggesting that they may be good candidates for active restoration during the first stages of the succession process. On the other hand, *H. madagascarensis* may form mono-specific stands of secondary forest (Schatz 2001) with subsequently negative effects on the establishment of other species, and should therefore be treated with care. *Albizia chinensis*, *F. baronii*, *C. mongue*, and *T. lastelliana* are more typical forest species, although only the two latter were found within the study forest plots. Their occurrence in the fallows suggests that these species may be good candidates for active restoration of degraded forest ecosystems in our study area because they have the ability both to establish rapidly after abandonment and to survive in a dense forest. The Fabaceae *A. chinensis* may be suitable for active restoration because of its N-fixing bacteria, which increase the levels of available N in the soil and thus may facilitate growth of other species (Guariguata and Ostertag 2001; Hughes and Denslow 2005; Bristow et al. 2007). Although all these species are widespread through Madagascar, only *C. mongue* is native (endemic) to Madagascar, which is crucial if the reference system for restoration is the primary forest. *Ficus baronii* and *H. madagascarensis* are native to central Africa, *Trema orientalis* and *A. chinensis* are both native to Asia, whereas the origin of *T. lastelliana* is, as far as we know, unknown. However, we recommend all these species to be further studied to examine their potential for restoration, i.e. if they have positive effects on the establishment of other tree species.

We found no relationship between the distance to the primary forest and tree seedling or sapling richness, abundance, or composition in Vohimana. This would not be a surprise if colonizing species were specialists of disturbed habitats rather than primary forest species, but our results show that both pioneers and forest species are among the first colonizers of the fallows. However, mechanical deforestation might eliminate live roots and seedbanks, but when the sites are cleared manually for cultivation without root removal, as in Vohimana, sprouting from stumps and roots are shown to be an important source of recruitment, in particular in the first stages of succession (e.g. Rouw 1993; Vieira and Proctor 2007). It is, however, expected that seed dispersal from the forest will be more important than resprout later in succession (Guariguata and Ostertag 2001). Then, a denser canopy may also allow more shade dependent forest species to establish. Seed predation is also an important factor in both tropical and temperate forests (see Guariguata and Ostertag 2001 and references therein), and experimental studies in cleared tropical forests in the Amazon have shown that tree recruitment from seeds is more likely to originate from the seed bank than from the seed rain (Uhl et al. 1982; Young et al. 1987; Lawton and Putz 1988), probably because most of the dispersed seeds are removed by animals (Uhl 1987). Overall, our results agree with those of Mitja et al. (2008) who suggested that in fallows following manual deforestation, with or without use of fire, pioneer and forest species establish simultaneously and grow together in the early succession after disturbance. This is in line with the reductionist succession model based on the Initial Floristic Composition of Eagler (1954). The alternative holistic model, on the other hand, which predicts that pioneer species establish first in disturbed areas, and subsequently facilitate the establishment of true forest species (Finegan 1984), may be more applicable after stronger mechanical disturbances when removal of roots and seedbank inhibit sprouting and germination of the original vegetation (Mitja et al. 2008).



The slash-and-burn system is deeply rooted in traditional agricultural practice in Madagascar, and elsewhere, and is thus likely to persist. At low yield-requirements it might have been a sustainable system. However, with an increasing yield-requirement, primarily due to increasing human population size, a shortening of fallow periods result in decreased longer term yields (Styger et al. 2007). This situation causes people to extend the agricultural area into primary and secondary forest. Alternatives to agricultural exploitation of ecosystems are currently being tried in Madagascar, but these take time to establish, and complimentary approaches are needed. Thus, increased yield of existing slash-and-burn areas is desired in order to prevent a further degradation of existing natural forest areas. Solutions, such as increased use of inorganic/organic fertilizer, changes to perennial crops (e.g. banana), and planting of exotic species (e.g. *Eucalyptus* for fuel wood) are used in many degraded forest ecosystems in eastern Africa, but these solutions are not optimal because they most often create monocultures that decrease ecosystem function and biodiversity dramatically. Our approach is to identify species that can be used in active restoration to speed up recovery time of fallows through species that both colonizes fallow areas early and that occur natural in forests. This study has identified six such species that we recommend being tested further. Seedlings can be collected from the surrounding forest or germinated from seeds, and planted into abandoned slash-and-burn areas in order to speed up natural succession. Transplants of seedlings have shown up to 90% survival in tropical Amazonia, but should be planted into fallows where some vegetation is already established, so that seedling survival is facilitated through shading (Uhl 1982, 1987). Establishment of natural forest vegetation could result in a quicker rehabilitation and built-up of soil nutrient stocks that make fallows usable within the needed time, such that the extension of cultivated areas into primary forest areas is prevented, or at least reduced.

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## References

- Brady NC (1996) Alternatives to slash-and-burn: a global imperative. *Agric Ecosyst Environ* 58:3–11
- Brearley FQ, Prajadinata S, Kidd PS, Proctor J, Suriantata (2004) Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. *For Ecol Manag* 195:385–397
- Bristow M, Vanclay JK, Brooks L, Hunt M (2007) Growth and species interactions of *Eucalyptus pellita* in a mixed and monoculture plantation in the humid tropics of north Queensland. *For Ecol Manag* 233:285–294
- Carrière SM, Letourmy P, McKey DB (2002) Effects of remnant trees in fallows on diversity and structure of forest regrowth in a slash-and-burn agricultural system in southern Cameroon. *J Trop Ecol* 18:375–396
- Dalle SP, de Blois S (2006) Shorter fallow cycles affect the availability of noncrop plant resources in a shifting cultivation system. *Ecol Soc* 11(2):2. <http://www.ecologyandsociety.org/vol11/iss2/art2/>
- Eagler FE (1954) Vegetation science concepts: I. Initial floristic composition, a factor in old field vegetation development. *Vegetatio* 4:412–417
- Faramalala MH, Rajeriarison C (1999) Nomenclature des formations végétales de Madagascar. ANGAP, Antananarivo, p 42
- Finegan B (1984) Forest succession. *Nature* 312:109–114
- Gade DW (1996) Deforestation and its effects in highland Madagascar. *Mt Res Dev* 16:101–116

- Gehring C, Denich M, Vlek PLG (2005) Resilience of secondary forest regrowth after slash-and-burn agriculture in central Amazonia. *J Trop Ecol* 21:519–527
- Grace J (2004) Understanding and managing the global carbon cycle. *J Ecol* 92:189–202
- Green GM, Sussman RW (1990) Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science* 248:212–215
- Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *For Ecol Manag* 148:185–206
- Houghton RA, Skole DL, Nobre CA, Hacker JL, Lawrence KT, Chometowski WH (2000) Annal fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature* 403:301–304
- Hughes RF, Denslow JS (2005) Invasion by a N-2-fixing tree alters function and structure in wet lowland forests of Hawaii. *Ecol Appl* 15:1615–1628
- Lawton RO, Putz FE (1988) Natural disturbance and gap-phase regeneration in a wind exposed tropical cloud forest. *Ecology* 69:764–777
- Lowry PP II, Schatz GE, Phillipson PB (1997) The classification of natural and anthropogenic vegetation in Madagascar. In: Goodman SM, Patterson BD (eds) *Natural change and human impact in Madagascar*. Smithsonian Institution Press, Washington, DC, pp 93–123
- Marcus RR (2001) Seeing the forest for the trees: integrated conservation and development projects and local perceptions of conservation in Madagascar. *Hum Ecol* 29:381–396
- Miller PM, Kauffman JB (1998) Seedling and sprout response to slash-and-burn agriculture in a tropical deciduous forest. *Biotropica* 30:538–546
- Mitja D, de Souza Miranda I, Velasquez E, Lavelle P (2008) Plant species richness and floristic composition change along a rice-pasture sequence in subsistence farms of Brazilian Amazon, influence on the fallows biodiversity (Benfica, State of Pará). *Agric Ecosyst Environ* 124:72–84
- Myers N, Mittermeier CG, DaFonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Oxby C, Boerboom JHA (1985) Alternatives and improvements to shifting cultivation on the east coast of Madagascar. In: FAO (ed) *Changes in shifting cultivation in Africa*, vol 50/1. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy, pp 109–139
- Rabemananjara F, Rasamison, Ramandimbison H (2003) Inventaire rapide de la faune herpétologique et entomologique avec diagnostic écologique du corridor forestier Vohimana et alentours. MATE, 21 p
- Randrianirina JE (2005) Inventaire biologique de la forêt de Vohimana et de Vohibola. Rapport de mission MATE, 37 p
- Roder W, Phengchanh S, Maniphone S (1997) Dynamics of soil and vegetation during crop and fallow period in slash-and-burn fields of northern Laos. *Geoderma* 76:131–144
- Rouw ADE (1993) Regeneration by sprouting in slash and burn rice cultivation. *J Trop Ecol* 9:387–408
- Sala EO, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sandwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, LeRoy Poff N, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Schatz GE (2001) *Generic tree flora of Madagascar*. Cromwell Press, UK, p 477
- Smith J, van de Kop P, Reategui K, Lombardi I, Sabogal C, Diaz A (1999) Dynamics of secondary forests in slash-and-burn farming: interactions among land use types in the Peruvian Amazon. *Agric Ecosyst Environ* 76:85–98
- Styger E, Rakotonramasy HM, Pfeffer MJ, Fernandes ECM, Bates DM (2007) Influence of slash-and-burn farming on fallow succession and land degradation in the rainforest region of Madagascar. *Agric Ecosyst Environ* 119:257–269
- ter Braak CJF, Smilauer P (2002) *CANOCO reference manual and CanoDraw for windows user's guide: software for canonical community ordination (version 4.5)*. Microcomputer Power, Ithaca, New York, US, p 500
- Uhl C (1987) Factors controlling succession following slash-and-burn agriculture in Amazonia. *J Ecol* 75:377–407
- Uhl C, Jordan C, Clark K et al (1982) Ecosystem recovery in Amazon caatinga forest after cutting, cutting and burning, and bulldozer clearing treatments. *Oikos* 38:313–320
- Vieira ICG, Proctor J (2007) Mechanisms of plant regeneration during succession after shifting cultivation in eastern Amazonia. *Plant Ecol* 192:303–315
- Young KR, Ewel JJ, Brown BJ (1987) Seed dynamics during forest succession in Costa Rica. *Vegetatio* 71:157–173