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Changes in diversity along a successional gradient in a Costa Rican upper montane *Quercus* forest

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Changes in terrestrial vascular plant diversity along a successional gradient were studied in a Costa Rican upper montane *Quercus* forest. In 1991 and 1992 species presence and cover were recorded in 12 successional 0.1 ha forest plots. A total of 176 species in 122 genera and 75 families were found. Asteraceae was the most speciose family. With the help of TWINSpan three successional phases were classified: (i) Early Secondary Forest (ESF, 145 spp.), (ii) Late Secondary Forest (LSF, 130 spp.) and (iii) Primary Forest (PF, 96 spp.). Detrended Correspondence Analysis (DCA) species ordination using DECORANA illustrates that different ecological species groups can be distinguished along the time sequence. Alpha diversity (Shannon-Wiener index, among others) in ESF and LSF was significantly greater than in PF. This is probably explained by downslope migration of numerous sub(alpine) species to cleared and recently abandoned montane sites. Beta diversity applying Sørensen's similarity coefficients declined during succession. Using linear regression, the minimum time required for floristic recovery following disturbance and abandonment was calculated at 65.9 years. A comparison with other studies shows that secondary forests in upper montane Costa Rica can be as diverse as in neotropical lowlands.

Keywords: Costa Rica; diversity; forest recovery; *Quercus*; secondary succession; tropical montane forest

Introduction

During the last three decades deforestation in tropical mountain regions has increased strongly (Budowski, 1968; Monasterio *et al.*, 1987). Clearing of tropical montane cloud forests has led to severe land degradation in general and to biodiversity depletion in particular (Monasterio *et al.*, 1987). However, until recently tropical montane forest recovery, secondary succession following clearing and biodiversity conservation in the upland tropics received little attention from scientists (Ewel, 1979, 1980; Gentry, 1982, 1988; Sugden *et al.*, 1985; Van der Hammen *et al.*, 1989; Brown and Lugo, 1990). The few studies presently available include an inventory of seral communities inhabiting

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abandoned 'old fields' in Mexican highlands (González-Espinosa *et al.*, 1991) and several assessments of mid-montane and lower montane forest recovery following clearing or severe hurricane damage in the Caribbean region (e.g. Byer and Weaver, 1977; Sugden *et al.*, 1985; Weaver, 1986; Walker *et al.*, 1991). However, the recovery patterns found in lowland and mid-montane tropical forests appear to be different from those observed in tropical upper montane forests near the upper forest line, where regrowth is extremely slow (Ewel, 1980). Therefore, changes in diversity during secondary succession following clearing and short-term grazing were studied in a Costa Rican upper montane *Quercus* dominated forest. This cloud forest is located in the Cordillera de Talamanca at about 3000 m elevation just below the upper forest limit. Here, successional phases of different ages were easily recognizable, assuming that they represent a true time sequence (Brown, 1992). The structure and the floristic composition of undisturbed, mature *Quercus* forest in the area were treated in detail at an earlier stage (Blaser, 1987; Jiménez *et al.*, 1988; Kappelle *et al.*, 1989, 1992; Orozco, 1991; Berner, 1992). The present paper is meant to contribute to a better insight in the trends in plant diversity following clearing of neotropical montane forests. Such knowledge is of utmost importance for its enormous potential in the development of programmes for the conservation of fragile tropical high-altitude ecosystems.

Materials and methods

Study Area

Twelve sites of similar altitude (2950–3050 m above sea level), slope aspect (SE to SW), slope inclination (25 to 35°) and soil type (Andosols) were selected near Jaboncillo de Dota in the upper watershed area of the Río Savegre. This protected river basin is located in the largely deforested 62 000 ha Los Santos Forest Reserve on the Pacific slope of the Costa Rican Cordillera de Talamanca (9°35'40" N, 83°44'30" W). The Cordillera, the 'backbone' of lower Central America, is made up of intrusive, and Tertiary volcanic rocks, alternating with marine sediments (Weyl, 1980; Castillo, 1984). Rock outcrops near Cerro de la Muerte (3491 m altitude) at 8 km SE of the investigated sites show evidence from glacial periods (Hastenrath, 1973). According to J.G. van Uffelen (personal communication) soils in the study area are mainly Humic (Mollic or Umbric) Andosols (FAO, 1977). Soil acidity at 15 cm soil depth ranges from pH 4 to pH 7 in secondary and degraded upper montane forests (Kappelle *et al.*, in press). The climate is very humid and cold, with the average annual temperature around 10.5°C (Herrera, 1986). In mature and recovering forests, temperatures ranged from 2 to 24°C in the dry season (February 20–24, 1992), and from 6 to 20°C in the wet season (August 20–24, 1992), while the relative humidity oscillated in the same periods between 35 and 95% (dry season) and 70 to 95% (wet season), (Kennis and De Vries, 1993). The average annual rainfall at 2960 m altitude near Ojo de Agua, just 4 km NW of the study sites, is about 2650 mm (IMN, 1988).

Site selection and data collection

Nine 0.1 ha plots (40 × 25 m) were established in patches of 8 to 32 y old secondary forests, which had developed on abandoned sites that shared the same land use history. According to oral information from different farmers, former land use included total clearing and burning of primary *Quercus* forest followed by a grazing period of three to eight years after which abandonment took place. Secondary forest plots were established in such a way that

the approximate distance to mature forest fragments ranged from 200 to 500 m, and the distance to upslope (sub)alpine vegetation from 1 to 3 km. This was done in order to reduce possible between-plot differences in seed input from patches of undisturbed vegetation. For matters of comparison three additional 0.1 ha plots were established in undisturbed primary (mature) forest at a minimum distance of 500 m from sites suffering from human impact.

In each plot the vertical (aerial) crown or shoot cover projection of each terrestrial vascular plant species was estimated using common vegetation-ecological procedures (Braun-Blanquet, 1965; Mueller-Dombois and Ellenberg, 1974; Kent and Coker, 1992). The growth form of each species was recorded. Shrubs were distinguished from trees as woody species with adult individuals having their first ramification below 1.3 m. Plant specimens were collected for subsequent identification at the Costa Rican National Herbarium (CR). Voucher specimens were stored in CR and U (collections by M. Kappelle, H.P. van Velzen and W.H. Wijtzes). Taxonomic nomenclature follows Burger (1971–1990), Standley (1937–1938), and Woodson and Schery (1943–1980) for angiosperms, and Lellinger (1989) and Tryon and Tryon (1982) for pteridophytes.

Data analysis and interpretation

Since multivariate statistics are most useful in describing and analysing species changes associated with successional gradients (Tueller and Platou, 1991), a polythetic divisive classification was undertaken with TWINSpan (Two Way Indicator Species Analysis; Hill, 1979b) on a data matrix (presence/absence and species-cover data) comprising 12 plots $\times$ 176 species occurring in at least two plots (Jongman *et al.*, 1987; Kent and Coker, 1992). For the purpose of classification, species cover percentages were converted into nine cover classes using an adapted form of the logarithmic octave-scaling technique proposed by Gauch (1982): 0% (–), < 1% (1), 1% (2), 2–3% (3), 4–7% (4), 8–15% (5), 16–31% (6), 32–63% (7), 64–100% (8). Next, the data matrix was ordinated by Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) using the DECORANA package (Hill, 1979a). On the basis of the outcomes of both multivariate data treatments, successional forest phases and ecological species groups were distinguished along the time sequence (Jongman *et al.*, 1987; Kent and Coker, 1992).

Dominance-diversity relationships were analysed for each successional phase, plotting relative cover values on a log-scale against species sequence or rank (Whittaker, 1965, 1975; Bazzaz, 1975). Species were ranked from high to low cover, in such a way that both species richness (on the X-axis) and evenness or equitability (slope of the curve) were shown in an illustrative way (Bazzaz, 1975).

Alpha diversity (within-habitat or within-phase diversity) was assessed for each plot and successional phase, using different diversity measures with varying sensitivities to rare and abundant species (Peet, 1974; Bazzaz, 1975; Pielou, 1975; Whittaker, 1975; Magurran, 1988; Van der Maarel, 1988). Therefore, species richness S (number of spp. per plot) and species density d (number of spp. in a plot per logarithmic unit area) were calculated and species-area relationships were analysed. Also, the following alpha diversity indices (measures of heterogeneity) were measured in order to take into account both evenness and species richness. First, the (information statistic) Shannon-Wiener index H' , which is most affected by rare species (Magurran, 1988), was calculated:

$$H' = - \sum (p_i) (\log_2 p_i) \quad (1)$$

where p_i is the proportional cover of the i^{th} species in a plot. Significant differences between the outcomes of H' for each of the different successional phases were searched for using parametric statistics. This is justified by the fact that H' values for a number of samples are normally distributed (Taylor, 1978). Significant differences were analysed with the help of Tukey-Kramer's honestly significant difference method, which is an unplanned multiple comparison test within the group of single classification (one-way) ANOVA techniques (Sokal and Rohlf, 1981; Magurran, 1988). This method was chosen, because the TWINSpan analysis revealed a set of three unequally-sized samples (containing five, four and three plots, respectively), each representing one successional phase. The Tukey-Kramer method was performed with help of SYSTAT (1992).

Evenness of species cover, i.e. the ratio of observed diversity to maximum diversity, was calculated using the Evenness or Equitability index E as follows (Peet, 1974; Pielou, 1975; Magurran, 1988):

$$E = H'/H_{\max} \quad (2)$$

where $H_{\max}$ is $\log_2 S$ and S is the number of species in a sample (plot).

Next, the reciprocal of the (dominance) Simpson index D was measured, using proportions of total percentages of vertical (aerial) crown or shoot cover projections (Simpson, 1949; Peet, 1974; Magurran, 1988). The reciprocal form $1/D$ was used in order to ensure that the value of the index rises with increasing diversity (Magurran, 1988):

$$1/D = 1/(\sum [p_i^2]) \quad (3)$$

With a view to understanding the temporal structuring of the successional phases, beta diversity (between-habitat or between-phase diversity) was calculated comparing secondary forest plots with plots in primary forest (Whittaker, 1972, 1975; Wilson and Shmida, 1984; Shmida and Wilson, 1985; Di Castri *et al.*, 1992). In this way the degree of turnover in species composition along the successional gradient was assessed (Pielou, 1975; Magurran, 1988), thus giving insight in the way secondary forests recover floristically. Since sampling plots were not exactly equidistantly spaced along the temporal gradient beta diversity was analysed as the degree of similarity between primary and secondary plots, using Sørensen's coefficient of community CC (Sørensen, 1948; Jongman *et al.*, 1987). For matters of reference similarity coefficients for pairs of primary forest plots were calculated. Thus, the level of floristic recovery of secondary forest stands was assessed as the recovery of floristic similarity between both secondary and primary forest phases. Sørensen's coefficient of community CC can be written as follows (Sørensen, 1948):

$$CC = 2c/(a + b + 2c) \quad (4)$$

where a is the number of species unique to plot A, b the number of species unique to plot B, and c the number of species shared by plots A and B.

Following Riswan *et al.* (1985) similarity values of species compositions of pairs of primary and secondary forest were extrapolated in time. In this way, the relationship between Sørensen similarity coefficients and time (period of recovery since abandonment) was studied for nine secondary forest plots as related to one primary forest plot. Similarity data were fitted to a linear regression equation to calculate the minimal time required for an abandoned pastureland to reach the mean similarity of a pair of two undisturbed primary (mature) forest stands (Jongman *et al.*, 1987).

Finally, a comparison was made with data available from tropical lowland and

temperate piedmont forests (Bongers *et al.*, 1988; Faber-Langendoen and Gentry, 1991; Purata, 1986a; Peet and Christensen, 1988; Toro and Saldarriaga, 1990).

Results

Successional phases and ecological species groups

In twelve 0.1 ha plots 176 species were found in 122 genera and 75 families (see appendix). These species were distributed among 52 trees, 19 shrubs, 52 herbs, 16 climbers, 1 bamboo, 34 ferns and 2 fern-allies. Vertical (aerial) crown (or shoot) cover values of species as estimated in the field ranged from < 1 to 85%. With the help of the TWINSPAN classification programme three successional phases were distinguished (Table 1): (i) an 8 to 20 y old Early Secondary Forest phase (ESF) dominated by *Fuchsia arborescens* and *Abatia parviflora* (five plots), (ii) a 25 to 32 y old Late Secondary Forest phase (LSF) dominated by *Quercus copeyensis* and *Q. costaricensis* (four plots) and (iii) an undisturbed Primary (mature) Forest phase (PF) dominated by the same species of oak as LSF (three plots). These forest phases fitted perfectly within earlier published descriptions of *Fuchsia-Abatia* and *Quercus* plant communities in the same region (Kappelle *et al.*, 1989 and in press; Kappelle, 1992). Therefore, no details with respect to their structure and floristic composition are given in the present study. The focus of this paper is rather on patterns in diversity in the light of forest succession. For that reason plant communities will be dealt with as successional forest phases.

Table 2 shows the spectrum of the successional forest phases as distributed over seven growth form types (trees, shrubs, herbs, climbers, bamboos, ferns and fern-allies). ESF includes 145 species, of which almost 30% are trees and over 30% herbs. The remaining 40% are mainly distributed among ferns (18%), shrubs (11%) and climbers (9%). Only one species of bamboo (*Chusquea tomentosa*) and one fern-ally (*Lycopodium clavatum*) were recorded in this phase. In LSF 130 species were recorded, with trees in a first and herbs in second place. Ferns come third, while shrubs remain near a tenth of the total. Climber diversity declines rapidly to half the number of species recorded in ESF. With only 96 species of terrestrial vascular plants PF is the most species-poor phase. PF is being dominated by trees, while herbs, climbers and ferns together contribute to two thirds of the total number of species. The reduction of herbs to half the number present in LSF is remarkable. Fern-allies were absent in PF.

DCA ordination of 176 species illustrates that five different ecological species groups can be recognized along the time sequence (DCA axis 1): (i) Pioneering, (ii) Early Successional and (iii) Late Successional Secondary Species, and (iv) Early and (v) Late Recovering Primary Species (Fig. 1). DCA axis 2 suggests a moisture gradient with pioneering species like *Abatia parviflora*, *Buddleja nitida*, *Cardamine bradei*, *Romanschulzia costaricensis* and *Salvia iodochroa* occupying drier sites (negative Y-values), and *Jungia ferruginea*, *Hydrocotyle bowlesioides*, *Piper bredemeyeri*, *Senecio copeyensis* and *Solanum incomptum* inhabiting wetter places (positive Y-values). Table 3 shows the spectrum of the five ecological species groups as distributed over the seven growth form types. Trees and ferns are equally distributed over secondary and primary species. Shrubs, herbs and climbers decrease in numbers as succession advances. This is most striking among herbs, which drop from 41 secondary species to 11 primary species. Apparently this phenomenon finds its origin in the invasion of herb species coming from mature tropical alpine and subalpine habitats (see Discussion).

Table 1. Vegetation table showing early and late secondary and primary upper montane forest in Costa Rica

successional phase (plant community)	early secondary forest	late secondary forest	primary forest	successional phase (plant community)	early secondary forest	late secondary forest	primary forest
approx. age (in y since aband.)	12102 20080	2333 5020	---	approx. age (in y since aband.)	12102 20080	2333 5020	---
plot number (01 to 12)	00000 12345	0000 6789	111 012	plot number (01 to 12)	00000 12345	0000 6789	111 012
TWINSpan division (upper part)	00000 00000 00000	0000 1111 1111	111 001 001	TWINSpan division (lower part)	00000 00000 00000	0000 1111 1111	111 001 001
161 plant species arranged in XVI ecological species groups	00001 0011	0011	---	161 plant species arranged in XVI ecological species groups	00001 0011	0011	---
I							
001 <i>Abatia parviflora</i>	54422	--1-	---	026 <i>Buddleja nitida</i>	56155	5-14	---
002 <i>Bocconia frutescens</i>	32131	---	---	027 <i>Monnina crepinii</i>	53351	2213	---
003 <i>Begonia udisivestris</i>	31121	1---	---	028 <i>Rubus eriocarpus</i>	51244	4-12	---
004 <i>Solanum costaricense</i>	31111	---	---	029 <i>Muehlenbeckia tamnifolia</i>	31145	411-	---
005 <i>Conyza bonariensis</i>	11112	---	---	030 <i>Arenaria lanuginosa</i>	41141	131-	1--
006 <i>Polypodium loriceum</i>	11111	1--	---	031 <i>Senecio multivenius</i>	31153	11-1	1--
007 <i>Jungia ferruginea</i>	2-434	---	---	032 <i>Halenia rhyacophylla</i>	11111	1-11	---
008 <i>Hydrocotyle ribifolia</i>	114-4	---	---	033 <i>Cirsium subcoriaceum</i>	1-121	1-11	---
009 <i>Alchemilla sibbaldifolia</i>	3-131	---	---	034 <i>Asplenium castaneum</i>	11111	1-1-	---
010 <i>Sibthorpia repens</i>	2-131	1--	---	035 <i>Valeriana scandens</i>	11111	-11-	---
011 <i>Oxalis spiralis</i>	2112-	--1-	---	036 <i>Geranium guatemalense</i>	11111	1-1-	---
012 <i>Thelypteris goeziana</i>	-2111	---	---	037 <i>Senecio copeyensis</i>	1-341	1-1-	1--
013 <i>Myosotis</i> sp.	1-111	---	---	038 <i>Plantago australis</i>	1-111	1-1-	---
014 <i>Solanum incompitum</i>	2-33-	---	---	039 <i>Viola nannei</i>	31-13	2--	---
015 <i>Sigesbeckia jorullensis</i>	31--1	--1-	---	040 <i>Calceolaria trilobata</i>	31--1	1-2	---
016 <i>Tropaeolum emarginatum</i>	111--	---	---	041 <i>Lobelia xalapensis</i>	11-11	1-1-	---
017 <i>Spiranthes</i> sp.	111--	---	---	042 <i>Ageratina kupperi</i>	2--43	3--	---
018 <i>Romanschulzia costaricensis</i>	11-1-	---	---	043 <i>Saurauia veraguasensis</i>	-11-2	1-1-	---
019 <i>Cardamine bradei</i>	11--1	---	---	044 <i>Stellaria irazuensis</i>	111--	--1-	---
020 <i>Mikania cordifolia</i>	1-11-	---	---	045 <i>Solanum</i> sp.	1-2-	-1--	---
021 <i>Polystichum muricatum</i>	1-11-	---	---	046 <i>Salvia todochroa</i>	11--	1-1-	---
022 <i>Salvia</i> sp.	1--3-	---	---	047 <i>Lycopodium clavatum</i>	--2-	--1-	---
023 <i>Piper bredemeyeri</i>	--1-1	---	---				
II							
024 <i>Fuchsia arborescens</i>	64263	432-	1-1	048 <i>Ageratina subcordata</i>	53454	5414	1-1
025 <i>Verbesina oerstediana</i>	54452	332-	---	049 <i>Fuchsia microphylla</i>	44345	5313	121

Table 1. (Continued)

successional phase (plant community)	early secondary forest	late secondary forest	primary forest	successional phase (plant community)	early secondary forest	late secondary forest	primary forest
approx. age (in y since aband.)	12102 20080	2333 5020	---	approx. age (in y since aband.)	12102 20080	2333 5020	---
plot number (01 to 12)	00000 12345	0000 6789	111 012	plot number (01 to 12)	00000 12345	0000 6789	111 012
TWINSPAN division (upper part)	00000 00000 00000	0000 1111 1111	111 001 001	TWINSPAN division (lower part)	00000 00000 00000	0000 1111 1111	111 001 001
161 plant species arranged in XVI ecological species groups	00001 0011	0011		161 plant species arranged in XVI ecological species groups	00001 0011	0011	
050 <i>Smilax kunthii</i>	23234	3415	111	074 <i>Escallonia myrtilloides</i>	--1-3	4-14	---
051 <i>Cornus disciflora</i>	55245	4434	1--	075 <i>Rumex acetosella</i>	1-1--	4-11	0011
052 <i>Monochaetum neglectum</i>	54335	5424	---	076 <i>Grammitis montiformis</i>	--1--	1111	---
053 <i>Acena elongata</i>	31254	5213	---	077 <i>Eriosorus flexuosus</i>	--1--	1-11	0011
054 <i>Castilleja talamancensis</i>	21133	3111	---	078 <i>Lycopodium thuyoides</i>	-----	13-3	0011
055 <i>Carex jamesonii</i>	11132	3111	---	079 <i>Senecio cooperi</i>	----1	3---	0011
056 <i>Gnaphalium attenuatum</i>	11111	1111	1--				
057 <i>Cestrum irazuense</i>	33-22	353-	-2-	080 <i>Centropogon gutierrezii</i>	-1211	-1-1	1--
058 <i>Alchemilla pascuorum</i>	11-22	3-13	---	081 <i>Malaxis hastilabia</i>	1-11-	1--	0100
059 <i>Pteridium aquilinum</i>	-1-53	3-12	---	082 <i>Solanum dotanum</i>	--21-	----	1--
060 <i>Erigeron karwinskianus</i>	1-112	-13	---				
061 <i>Lachemilla pectinata</i>	11-1-	-111	---	V1			
062 <i>Polypodium macrolepis</i>	111--	-111	---	083 <i>Oreopanax xalapense</i>	24133	3322	0101
063 <i>Campyloneurum amphostenon</i>	11--1	11-1	---	084 <i>Centropogon costaricae</i>	21243	131-	0101
064 <i>Hedyosmum mexicanum</i>	-11-3	-41-	---	085 <i>Roldana heterogama</i>	12111	1211	0101
065 <i>Galium mexicanum</i>	-11--	-111	---	086 <i>Bomarea acutifolia</i>	12131	2111	0101
066 <i>Centropogon irazuensis</i>	21-1-	-3--	---	087 <i>Peperomia alpina</i>	11111	1111	0101
067 <i>Grammitis meridenis</i>	-1---	-1-	---	088 <i>Asplenium polyphyllum</i>	-11-1	11-1	0101
068 <i>Senecio oerstedianus</i>	--1--	---	---	089 <i>Passiflora membranacea</i>	111--	-1-1	-1-
069 <i>Clusia palmana</i>	----	1--	---	090 <i>Polystichum fournieri</i>	-1-11	--2	0101
				091 <i>Symplocos serrulata</i>	-111-	-1-	0101
				092 <i>Uncinia hamata</i>	-11--	1-1-	0101
				093 <i>Pleopeltis macrocarpa</i>	-11-	-1-1	0101
IV 070 <i>Conarostaphylis arbutoides</i>	--123	5434	-2-	094 <i>Myrcianthes fragrans</i>	---	-1-	0101
071 <i>Pernettya prostrata</i>	2--3-	4233	---	095 <i>Blechnum costaricense</i>	---	-1-	0101
072 <i>Garrya laurifolia</i>	11--3	21-4	---		--1-1	--1-	0101
073 <i>Hesperomeles heterophylla</i>	--113	3-13	---	VII			
				096 <i>Dryopteris wallichiana</i>	23212	3223	0110

Table 1. (Continued)

successional phase (plant community)	early secondary forest	late secondary forest	primary forest	successional phase (plant community)	early secondary forest	late secondary forest	primary forest
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TWINSpan division (upper part)	00000 00000 00000	0000 1111 1111	111 001 001	TWINSpan division (lower part)	00000 00000 00000	0000 1111 1111	111 001 001
161 plant species arranged in XVI ecological species groups	00001 0011	0011		161 plant species arranged in XVI ecological species groups	00001 0011	0011	
097 <i>Rhynchospora aristata</i>	11222	3313	111	XI 119 <i>Polypodium plebejum</i>	-1-1	11-1	111
098 <i>Ilex discolor</i>	-1222	131-	-11	120 <i>Ocotea pittieri</i>	-1-12	23--	134
099 <i>Myrsine pellicodopunctata</i>	1--24	35-5	-33	121 <i>Symplocos austinsmithii</i>	-----	-5-3	-45
100 <i>Ocotea mollicella</i>	--1--	-2--	--1	122 <i>Peperomia saligna</i>	-----	-111	-11
VIII 101 <i>Myrsine coriacea</i>	13115	6434	112	123 <i>Arachniodes denticulata</i>	-----	1-1-	-11
102 <i>Macleania rupestris</i>	11122	3423	112	124 <i>Persea vesticula</i>	-----	---2	-11
IX 103 <i>Chusquea tomentosa</i>	76767	6757	777	XII 125 <i>Miconia schnellii</i>	1-2-2	----	31-
104 <i>Miconia tonduzii</i>	-2-4	2-1-	121	126 <i>Lopezia paniculata</i>	-1---	----	1--
105 <i>Solanum storkii</i>	2---5	13--	-22	XIII 127 <i>Syrax argenteus</i>	11113	2433	644
X 106 <i>Quercus copeyensis</i>	21346	7875	888	128 <i>Ardisia costaricensis</i>	-3112	3525	466
107 <i>Quercus costaricensis</i>	31214	3547	755	129 <i>Ilex pallida</i>	--132	43-2	344
108 <i>Cleyera theaeoides</i>	44334	4545	545	130 <i>Zanthoxylum scheryii</i>	111--	2221	333
109 <i>Weinmannia pinnata</i>	25-44	4544	565	131 <i>Oreopanax capitatus</i>	-1-11	1211	331
110 <i>Viburnum costaricanum</i>	35135	5443	444	132 <i>Elaphoglossum furfuraceum</i>	-1---	-111	311
111 <i>Vaccinium consanguineum</i>	12122	3334	533	133 <i>Elaphoglossum squamipes</i>	--1--	-2--	111
112 <i>Peperomia quadrifolia</i>	-1111	1111	111	134 <i>Peperomia tetraphylla</i>	-----	1-1-	111
113 <i>Vriesia williamsii</i>	111--	1221	121	135 <i>Adiantum tenerum</i>	-----	--1-	1--
114 <i>Polypodium myriolepis</i>	11--1	1111	111	XIV 136 <i>Elaphoglossum hirtum</i>	11111	1111	115
115 <i>Campyloneurum fasciale</i>	-11--	1111	111	137 <i>Palicourea salicifolia</i>	1-111	13-1	354
116 <i>Elaphoglossum erinaceum</i>	1-1-1	11-1	-11	138 <i>Rhannus oreodendron</i>	---3	1211	244
117 <i>Ardisia compressa</i>	21---	--12	-3-	139 <i>Asplenium cuspidatum</i>	-1---	1---	-11
118 <i>Maianthemum paniculatum</i>	----1	1---	-1-	140 <i>Stellaria ovata</i>	-1---	--1-	-11

Table 1. (*Continued*)

successional phase (plant community)	early secondary forest	late secondary forest	primary forest	successional phase (plant community)	early secondary forest	late secondary forest	primary forest
approx. age (in y since aband.)	12102 20080	2333 5020	--- ---	approx. age (in y since aband.)	12102 20080	2333 5020	--- ---
plot number (01 to 12)	00000 12345	0000 6789	111 012	plot number (01 to 12)	00000 12345	0000 6789	111 012
TWINSpan division (upper part)	00000 00000 00000	0000 1111 1111	111 001 001	TWINSpan division (lower part)	00000 00000 00000	0000 1111 1111	111 001 001
161 plant species arranged in XVI ecological species groups	00001 0011	0011		161 plant species arranged in XVI ecological species groups	00001 0011	0011	
XV 141 <i>Anthurum concinatum</i>	---11	111-	355	152 <i>Oreopanax rubigenus</i>	-----	-----	-32
142 <i>Schefflera rodriguesiana</i>	-----	-11-	355	153 <i>Hydrangea asterolasia</i>	-----	-----	-23
143 <i>Prunus annularis</i>	-----	-----	232	154 <i>Fuchsia splendens</i>	-----	-----	-31
144 <i>Elaphoglossum hoffmannii</i>	---1	-----	311	155 <i>Hymenophyllum consanguineum</i>	-----	-----	-12
145 <i>Solenophora calycosa</i>	-----	-----	111	156 <i>Borychium virginianum</i>	-----	-----	11-
146 <i>Neomirandea angularis</i>	-----	-----	111	157 <i>Nectandra cufodontisii</i>	-----	-----	1-1
147 <i>Vitaria graminifolia</i>	-----	-----	111	158 <i>Pilea gracilipes</i>	-----	-----	-11
148 <i>Elaphoglossum</i> sp.	-----	-1-	111	159 <i>Chimaphila maculata</i>	-----	-----	-11
149 <i>Elaphoglossum latifolium</i>	-----	-----	-36	160 <i>Cavendishia bracteata</i>	---1-	-----	-11
150 <i>Asplenium serra</i>	--1-	-1-	-34				
151 <i>Drimys granadensis</i>	-----	-1-	-33	XVI 161 <i>Magnolia sororum</i>	-----2	-----	-3-

Table 2. Number of terrestrial vascular plant species per growthform for three successional phases in Costa Rican upper montane forests

Successional phase	Growth form ^a							Total
	T	S	H	C	B	F	FA	
Early secondary forest	43	16	45	13	1	26	1	145
Late secondary forest	43	12	40	6	1	26	2	130
Primary forest	39	9	20	5	1	22	0	96
Total	52	19	52	16	1	34	2	176

^aT = trees, S = shrubs, H = herbs, C = climbers, B = bamboos, F = ferns, FA = fern-allies.

A look at presence-absence data showed that fifteen out of 176 species were found in only one plot and could be termed 'rare'. They were omitted from Table 1 and are listed here: *Ardisia glandulosomarginata* (plot 5, cover 3%), *Bidens reptans* (3, 1%), *Cynanchum glaberrimum* (5, 1%), *Hydrocotyle bowlesioides* (8, 1%), *Miconia* sp. (11, 1%), *Mikania iltisii* (5, 2%), *M.* sp. (8, 1%), *Ocotea calophylla* (8, 1%), *Palicourea adusta* (11, 1%), *Passiflora mollissima* (3, 1%), *Pityrogramma chrysoconia* (8, 1%), *Polypodium* sp. (4, 1%), *Roldana scandens* (7, 1%), *Symplocos irazuensis* (2, 1%), and *Thibaudia costaricensis* (12, 6%). The small number of rare species implies that over 90% of the total number of species occurred in at least two out of 12 plots (i.e. with a minimum frequency of 16.7%). Another interesting observation is the high percentage of rare Asteraceae (four out of 15).

Most speciose families were Asteraceae (13 genera, 20 spp.) and Polypodiaceae (4 genera, 10 spp.). Lomariopsidaceae and Rosaceae were both represented by seven species, Ericaceae and Solanaceae each by six species, and Lauraceae, Myrsinaceae and Piperaceae each by five. Species-rich genera were *Elaphoglossum* (7 spp.), *Polypodium* (5), *Solanum* (5 spp.), *Asplenium* (4 spp.), *Peperomia* (4 spp.) and *Senecio* (4 spp.). *Asplenium*, *Elaphoglossum*, *Peperomia* and *Polypodium* were also found as epiphytes (M. Kappelle, unpublished results), suggesting that several of the congeneric species listed here as terrestrials probably behave as accidental rather than as obligate ground-rooted taxa (Benzing, 1990; Wolf, 1993).

Three dominance-diversity curves representing successional forest phases show a decrease in species richness and evenness as succession proceeds (Fig. 2). Their approximate log-normal distribution reflects the presence of few strongly dominant species (high relative cover values) in association with a large set of occasional species with low abundances (low relative cover values).

Trends in alpha diversity

Species richness and species density decreased with successional progress. Richness ranged from 91 to 100 terrestrial vascular plant species in ESF, from 75 to 90 in LSF and from 62 to 79 in undisturbed PF (Table 4). Density changed in a similar way since plot sizes were equal and density was calculated as a size-dependent derivate of richness. Figure 3 shows a cumulative increase in species number for each successional forest phase, each time a 0.1 ha plot is added. The logarithmic species-area relationship indicated a similar pattern for both ESF and LSF. While their cumulative species numbers continued to rise after adding two or three plots, species numbers in PF level off after adding one or two plots. Although plot sizes of 0.1 ha are recommended for tropical secondary forests

Figure 1. DCA ordination of 176 terrestrial vascular plant species in five ecological species groups: Pioneerizing secondary species (crosses), Early successional secondary species (open squares), Late successional secondary species (closed circles), Early recovering primary species (open circles) and Late recovering primary species (closed squares). Eigenvalues are 0.46 for DCA axis 1 (X-axis) and 0.08 for DCA axis 2 (Y-axis).

(Purata, 1986b) they appear to be relatively small. Yet secondary forest patches of a larger size, e.g. 0.2 or 0.5 ha, were not present in the study area.

Alpha diversity indices decreased with increasing time since abandonment. Diversity of terrestrial vascular plants was lowest in undisturbed PF (Table 4). The Shannon-Wiener index H' dropped from 5.06–5.39 in ESF and 4.63–5.2 in LSF to values below 4.5 in PF. H' was lowest in PF plot 10. The one-way Tukey-Kramer ANOVA test applied to H' values indicated that PF was significantly less diverse than ESF ($p < 0.001$) and LSF ($p < 0.05$). ESF and LSF did not differ significantly from each other. Simpson's reciprocal ($1/D$) also showed a decline in diversity with increasing time of recovery: from 11.19–24.42 in ESF to 6.34–17.68 in LSF, and 6.3–11.31 in PF. The Evenness or Equitability Index E changed similarly (Table 4).

Estimation of the minimum time of floristic recovery using beta diversity

Table 5 shows that the lowest Sørensen's Coefficient of Community (CC) calculated (0.37) corresponds to the floristic similarity between early secondary plot 1 and primary forest

Table 3. Numbers of terrestrial vascular plant species per growthform for five ecological species groups in Costa Rican upper montane forests. Roman numbers between brackets refer to species groups as listed in Table 1

Ecological species group	Growth form ^a							Total
	T	S	H	C	B	F	FA	
Secondary species	26	14	41	14	0	17	2	114
i Pioneering (I, II)	11	4	24	9	0	5	1	54
ii Early successional (III, IV)	8	8	10	3	0	7	1	37
iii Late successional (V, VI, VII, VIII)	7	2	7	2	0	5	0	23
Primary species	26	5	11	2	1	17	0	62
iv Early recovering (IX, X, XI, XII)	13	1	4	0	1	5	0	24
v Late recovering (XIII, XIV, XV, XVI)	13	4	7	2	0	12	0	38
Total	52	19	52	16	1	34	2	176

^aT = trees, S = shrubs, H = herbs, C = climbers, B = bamboos, F = ferns, FA = fern-allies.

plot 12. This value represents the highest measure of beta diversity found along the successional sere. The highest similarity measured between a late secondary and a primary forest plot reached 0.64, while the similarity between one pair of primary forest plots is only slightly higher (0.67). This means that a site, which today sustains a 30 years old LSF, is recovering floristically quite well.

The theoretical minimum time of an ‘acceptable’ floristic recovery was calculated as the number of years required for a secondary forest plot to become floristically as similar to a primary forest plot as the level of similarity between the average pair of primary forest

Figure 2. Dominance-diversity curves for three different successional forest plots in upper montane Costa Rica: Early secondary forest plot 3 (closed circles), Late secondary forest plot 7 (crosses) and Primary forest plot 12 (open circles). Species are ranked from high to low cover (X-axis) vs. their cover (Y-axis). For reasons of clarity, the curve for plot 7 has been shifted five positions to the right, and the curve for plot 12 thirty positions to the right.

Table 4. Five measures of alpha diversity as calculated for twelve 0.1 ha plots in three successional phases of Costa Rican upper montane forest. Means and standard-errors (SE) are given

Successional phase	Plot no.	Alpha	Diversity	Measure ^a		
		<i>S</i>	<i>d</i>	<i>H'</i>	1/ <i>D</i>	<i>E</i>
Early secondary forest	01	91	30.3	5.07	17.17	0.78
	02	91	30.3	5.06	15.50	0.78
	03	98	32.6	5.19	11.19	0.78
	04	91	30.3	5.39	24.42	0.83
	05	100	33.3	5.39	22.37	0.81
	Mean	94.2	31.4	5.22	18.13	0.80
	± 1 SE	1.8	0.6	0.07	2.13	0.01
Late secondary forest	06	90	30.0	5.20	17.68	0.80
	07	75	25.0	4.73	11.71	0.76
	08	90	30.0	4.63	7.85	0.71
	09	75	25.0	4.74	6.34	0.76
	Mean	82.5	27.5	4.83	10.90	0.76
	± 1 SE	3.8	1.3	0.11	2.19	0.02
	10	62	20.7	3.70	6.30	0.62
Primary forest	11	79	26.3	4.45	9.97	0.71
	12	68	22.7	4.38	11.31	0.72
	Mean	69.7	23.2	4.18	9.19	0.68
	± 1 SE	4.1	1.4	0.24	1.22	0.03

^a*S* = species richness, *d* = species density, *H'* = Shannon-Wiener index, 1/*D* = reciprocal Simpson index, *E* = Equitability index.

plots. For this purpose, Sørensen's *CC* values for nine secondary forest plots as related to primary forest plot 12 were fitted to a linear regression equation (Fig. 4):

$$Y = 0.31357 + 0.0071542 X \quad (5)$$

$$(n = 9, r^2 = 0.657, p < 0.01)$$

where *Y* is the beta diversity measured as Sørensen's Coefficient of Community and *X* is the time in years. By solving for *X* where *Y* is the mean similarity of 0.785 for a pair of undisturbed PF plots, the time required for the floristic similarity between a secondary and a primary forest to reach the floristic similarity found between two primary forests is 65.9 years. However, one must take into account, that *r*² equals 0.657 and that therefore 34.3% of the total variance of *Y* before regression remains unexplained.

Discussion

Trends in diversity along the successional gradient

Both the TWINSPLAN classification and the DECORANA ordination recognize successional progress as the main gradient under study. A series of twelve 0.1 ha plots is divided in three successional forest phases, while a set of 176 species is principally ordered along a forest recovery gradient (DCA axis 1). Ordination reveals a second axis (DCA axis 2), which probably corresponds to a moisture gradient. This becomes most apparent among Pioneer Secondary Species, which inhabit either wetter or drier places, such as in

Figure 3. Relationship between cumulative number of terrestrial vascular plant species and cumulative number of 0.1 ha plots for three successional forest phases in upper montane Costa Rica: Early secondary forest (open squares; 5 plots), Late secondary forest (closed circles; 4 plots) and Primary forest (closed squares; 3 plots).

relatively open environments. It is evident that great microclimatic differences existing over short topographical ranges disappear during secondary succession: as the canopy of later forest phases closes, moisture levels in the forest interior become more stable.

An important result from the present ecological study is the significant decrease in plant diversity as secondary succession advances. The outcomes of the different diversity measures substantiate this trend and confirm results from earlier research in the study area on arboreal recovery following forest clearing in a chronosequence of 0.05 ha plots (Kappelle, 1993), and on recovery of the ground layer vegetation in montane oakforest following selective logging (A. Schumacher, unpublished results). Alpha diversity differences between LSF and PF were smaller in Simpson's reciprocal than in the Shannon-Wiener values. A possible reason for this discrepancy is the similar abundance of the most common species in these two successional phases (keeping the Simpson index similar), while the number of rare species is higher in LSF (affecting the Shannon-Wiener index seriously). The Evenness or Equitability Index E changes in a similar way as the Shannon-Wiener index, and emphasizes once more the drop in diversity along the successional gradient, taking into account the relation between the actual diversity H' and the maximum possible diversity $H_{\max}$.

According to Bazzaz (1975) a high species diversity in secondary forests may be explained by a high degree of vertical and horizontal micro-environmental heterogeneity (high niche differentiation) in young successional forests. The complex layering (vertical) and the open canopy (horizontal) of the studied secondary forests contribute to a high level of spatial heterogeneity, but still do not fully explain the observed drop in diversity along

Table 5. Beta diversity expressed in floristic similarity values (Sørensen's Coefficients of Community) for pairs of forest plots in upper montane Costa Rica. Means and Standard-errors (SE) are given

	Primary forest plot			
	10	11	12	Mean $\pm$ 1 SE
Secondary forest plot				
01	0.42	0.38	0.37	0.39 $\pm$ 0.013
02	0.54	0.44	0.40	0.46 $\pm$ 0.034
03	0.56	0.43	0.41	0.47 $\pm$ 0.056
04	0.48	0.42	0.40	0.43 $\pm$ 0.020
05	0.53	0.48	0.42	0.48 $\pm$ 0.026
06	0.58	0.54	0.54	0.55 $\pm$ 0.011
07	0.64	0.60	0.61	0.62 $\pm$ 0.010
08	0.58	0.53	0.50	0.54 $\pm$ 0.019
09	0.54	0.54	0.51	0.53 $\pm$ 0.008
Primary forest plot				
10	—	0.67	0.71	0.69 $\pm$ 0.014
11	0.67	—	0.86	0.76 $\pm$ 0.067
12	0.71	0.86	—	0.79 $\pm$ 0.053

the time gradient. Looking at the flora of the secondary forests, and especially at the flora of ESF, one notes the presence of a large number of plant taxa well-known from upslope vegetation belts (Cleef and Chaverri, 1992). Many secondary montane forest species occur in primary subalpine (dwarf) forest and paramo vegetation above the upper forest line rather than in primary montane forests (Kappelle *et al.*, 1991; A.M. Cleef and A. Chaverri, unpublished results). Some of these are the arboreal *Abatia parviflora*, *Buddleja nitida*, *Comarostaphylis arbutoides*, *Escallonia myrtilloides*, *Fuchsia arborescens*, *Garrya laurifolia* and *Verbesina oerstediana*, which are all very abundant in subalpine primary forest communities between 3200 and 3400 m altitude (Kappelle *et al.*, 1991). Other woody species present in montane secondary forests dominate subparamo and paramo communities under natural conditions. These include *Acaena elongata*, *Ageratina kupperi*, *Cestrum irazuense*, *Hesperomeles heterophylla* and *Pernettya prostrata*. Herbs such as *Alchemilla pascuorum*, *Castilleja talamancensis*, *Gnaphalium attenuatum*, *Senecio oerstedianus* and *Viola nannei* and ferns like *Eriosorus flexuosus* and *Grammitis moniliformis* can also be considered paramo taxa (A.M. Cleef and A. Chaverri, unpublished results). Together these species form an important tropic (sub)alpine element in montane secondary forests. They are adapted to open environments, apparently provide a more stable micro-environment and create favourable conditions for the establishment of fastly-recovering primary forest taxa, such as the predominant *Chusquea*, *Cleyera*, *Quercus*, *Vaccinium* and *Weinmannia*. Later on, as canopy closure takes place, these taxa appear to outcompete the light-demanding taxa from (sub)alpine origin, a phenomenon well-illustrated by the changing dominance-diversity curves. Only a small amount of montane species can be characterized as truly secondary since they are also found in natural treefall gaps in mature forest (*Begonia udisilvestris*, *Oreopanax xalapensis*, *Piper*

Figure 4. Relationship between mean floristic similarity values (Sørensen's Coefficient of Community) for pairs of secondary and primary forest plots, and time (i.e. the period of recovery following disturbance and abandonment) in upper montane Costa Rica.

brede-meyeri, *Saurauia veraguasensis* and *Solanum dotanum*). Generally, through montane forest logging a large, harsh environment is created to which (sub)alpine plant species are better adapted than true montane forest gap-phase species, which inhabit the smaller natural treefall gaps in the inner primary forest.

Denslow (1980) suggested that between-community variations in diversity patterns during succession are due to the effects of selection among life history strategies under different disturbance regimes. In the present study montane PF probably represents a community or phase in which large-scale disturbances were historically rare (on the evolutionary time scale). Therefore, under natural conditions, the PF phase is characterized by a large number of species that reach the canopy through small gaps and relatively few species which regenerate in larger clearings. On the other hand, the subalpine forest and paramo vegetation include communities in which the greatest patch area is in large-scale disturbed areas, e.g. following extensive fire (Janzen, 1973; Horn, 1989, 1990). These communities are most diverse in species establishing seedlings in xeric and strong light conditions. As the secondary forest patches near 3000 m altitude are close to montane mature forest stands as well as to (sub)alpine vegetation patches, an intertwining complex of different successional pathways originates. In accordance with Denslow's theory, species diversity in successional phases of tropical upper montane forest is initially high, especially due to the high number of seedlings of possibly disturbance-adapted (sub)alpine species in the early stages of recovery (Denslow, 1980). Moreover, while Brown and Lugo (1990) already mention the general potential of tropical secondary forests as species refugia, one might consider (early) secondary phases of neotropical

Table 6. Measures of alpha diversity from this study compared to data available from other secondary and primary forests in the American tropics and northern temperate zone

	Alpha diversity measure ^a			
	<i>S</i>	<i>d</i>	<i>H'</i>	1/ <i>D</i>
Tropical montane forest				
Costa Rica				
15 y old secondary ^b	94	31.4	5.22	18.13
30 y old secondary ^b	83	27.5	4.83	10.90
mature primary ^b	70	23.2	4.18	9.19
Tropical lowland forest				
Mexico				
11 y old secondary ^c	39	16.9	5.1	—
20 y old secondary ^c	42	18.3	5.3	—
mature primary ^d	234	58.5	5.12	13.51
Colombia – Venezuela				
Río Negro				
14 y old secondary ^e	56	19.0	4.63	16.67
30 y old secondary ^e	77	26.1	5.18	25.00
80 y old secondary ^e	79	26.8	5.02	33.33
mature primary ^e	66	22.3	5.45	20.00
Colombia				
Amazonia				
9 y old secondary ^f	—	—	5.62	36.26
mature primary ^f	—	—	6.50	61.70
Chocó				
mature primary ^g	137	45.7	6.33	—
Temperate piedmont forest				
USA				
20–40 y old sec. pine ^h	51	17.0	2.72	9.6
mature prim. hardwood ^h	53	17.5	2.89	11.8

^a*S* = species richness, *d* = species density, *H'* = Shannon-Wiener index, 1/*D* = reciprocal Simpson index.

^bThis study, averaged for 0.1 ha (all terrestrial vascular plants).

^cPurata (1986) for 0.02 ha (ferns and fern-allies excluded).

^dBongers *et al.* (1988) for 1 ha (ferns and fern-allies excluded); indiv. ≥ 0.5 m high only).

^eSaldarriaga *et al.* (1988) for three 0.03 ha plots (tree stems ≥ 1 cm dbh).

^fToro and Saldarriaga (1990) for 0.01 ha of 9 y old secondary forest, and 0.25 ha of mature primary forest on sedimentary plains.

^gFaber-Langendoen and Gentry (1991) for (the mean of two plots of) 0.1 ha (woody stems ≥ 2.5 cm dbh).

^hPeet and Christensen (1988) for 0.1 ha (all terrestrial vascular plants).

montane forests as possible temporal refugia for specific subalpine and alpine (paramo) species possibly threatened in their original habitat.

In view of these patterns an important factor influencing secondary succession is seed availability, controlled by, for example, the distance from a recovering site to different

seed sources (Van der Maarel, 1988), or by the prevailing wind direction (M.J.A. Werger, personal communication). A cleared and recently abandoned site may be closer to (sub)alpine vegetation than to nearby mature forest fragments. Second, the isolated position of a recovering site within a matrix of intensively-grazed pasturelands is quite different from a site bordering other recovering forest stands in different phases of succession. Although study sites (plots) were selected at distances from 200 to 500 m to mature forest fragments and at about 1 to 3 km from (sub)alpine vegetation patches, it is not certain whether the selected sites are completely independent from this parameter. Especially differences in seed dispersal strategies, wind dispersal predominating in páramo species versus bird and mammal dispersal in mature montane forest species, may have played an important role in the propagule input at the study sites (W.H. Wijtzes, unpublished results).

Floristic recovery: towards the mature forest phase

From the present study it becomes clear that a large-scale disturbance such as clear-cutting may greatly affect the local species composition of a neotropical montane forest. Although levels of diversity rise relatively fast, the rate of floristic recovery is relatively slow. At least a period of 65 years following total clearing, burning, three to eight years of extensive cattle-grazing and subsequent abandonment are needed to reestablish a terrestrial vascular flora sufficiently similar to that of a mature forest. More decades are needed for a complete recovery of the floristic composition, and probably centuries are needed if recovery follows a logarithmic trend instead of a linear one along the time gradient. Future sampling of forest patches which could recover during a period of 40 to 80 years since abandonment is needed in order to understand the trends in secondary succession on the long term. However, today no such secondary forest stands are available, since deforestation in the study area started only in the 1950s (Kappelle *et al.*, in press). In order to follow this recovery process in a more detailed manner we propose to monitor the secondary forest plots sampled in the present study. In studies of biomass recovery after clearing Riswan *et al.* (1985) and Saldarriaga (1985; Saldarriaga *et al.*, 1988) estimate that periods of 100 to 200 years are needed as the minimum time required for tropical lowland forest to recover. In this study only data on floristic composition were used in order to estimate the minimum time of recovery. As a result of extremely slow growth rates prevailing at 3000 m above sea level (Ewel, 1980) it is expected that the recovery of the montane forest structure will take much longer than the mere floristic recovery.

At sites where land use practices were more destructive in the past, the recovery and resilience potential has probably been reduced severely. There, succession has possibly proceeded much slower and followed the path of retrogression (Ewel, 1983). In the case of a higher grazing intensity, e.g. a grazing period of ten to 20 years, soils would probably be much more compact due to cow trampling and erosion caused by heavy rainfall. This would affect the successful development of species germinating either from seeds stored in the local seedbank or from propagules coming in from nearby seedsources like mature forest fragments or remnants of primary forest trees (Ewel, 1983; Uhl and Clark, 1983; Guevara *et al.*, 1986; Brown and Lugo, 1990). A return to the initial or predisturbance floristic composition would then become impossible and long-term ecosystem degradation irreversible.

Comparison with tropical lowland and temperate piedmont forests

A comparison was made with results from studies on plant diversity along successional gradients in other tropical and temperate forest regions (Table 6). The following diversity measures were included in the comparison: species richness S , species density d , Shannon-Wiener's H' , and Simpson's reciprocal $1/D$. Plot sizes used by different authors ranged from 0.02 to 1 ha. Thus, the area-related species density d resulted in a better measure for comparison than the species richness S .

The most species-dense sites were found in mature lowland forests in Mexico (Bongers *et al.*, 1988) and South America (Chocó: Faber-Langendoen and Gentry, 1991; but see also Colombian and Ecuadorian Amazon region, J. Duivenvoorden and H. Lips [personal communication] and R. Valencia [personal communication]). These neotropical lowland rain forests are two or three times as dense in species (number ha^{-1}) as the mature primary *Quercus* forests here-studied. However, these Costa Rican forests in their turn are more species-dense than temperate (North American) piedmont forests (Peet and Christensen, 1988). On the other hand, a 15 year old secondary montane forest in Costa Rica was more diverse than early secondary forests along the Río Negro (Saldarriaga *et al.*, 1988) and in the Mexican Los Tuxtlas region (Purata, 1986a). At first sight this looks rather surprising, but may be explained by the above-described phenomenon of down-slope migration of tropic alpine and subalpine species into cleared montane forest sites. Moreover, Saldarriaga *et al.* (1988) treated only woody stems with $\text{dbh} \geq 1$ cm and Purata (1986a) did not include ferns and fern-allies, while the present study concerns all terrestrial vascular plants. Purata (1986a) suggested that, if disturbance in a Mexican lowland rain forest favours the occurrence of ruderal species, succession will be retarded. Secondary herb and shrub species in Mexican regrowth may hamper the establishment of pioneer tree species (inhibition), thus reducing diversity in the early phases. Thus, it seems, that primary, mature neotropical upper montane forests are less diverse in terrestrial vascular plant species than undisturbed neotropical lowland forests, but that secondary forests, on the other hand, may reach similar or even higher levels of diversity in neotropical upper montane forests than in neotropical lowland forests.

Implications for conservation

The present results show that montane secondary forests can play a major role in the conservation of the tropical mountain biome, since they harbour a wealth of plant species which are becoming endangered in their original habitat upslope. This is especially true for tropical alpine (paramo) and subalpine herb species which flourish in the early stages of montane secondary forests that recover from clearing and subsequent grazing. Moreover, their presence enhances the establishment of later successional species which are responsible for the success of the forest recovery process.

The advantage of speeding-up secondary succession through the invasion of plant species from harsh sites upslope seems restricted to tropical mountain ecosystems. The question remains, however, whether there is a similar invasive power that positively influences the process of forest recovery in the tropical lowlands, or that it is a truly unique phenomenon limited to the tropical mountain biome. Yet, the comparison (Table 6) among alpha diversity measures found in tropical montane and lowland forests of primary and secondary origin suggests the latter.

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References

- Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in Southern Illinois. *Ecol.* **56**, 485–8.
- Benzing, D.H. (1990) *Vascular epiphytes*. Cambridge: Cambridge University Press.
- Berner, P.O.B. (1992) Effects of slope on the dynamics of a tropical montane oak-bamboo forest in Costa Rica. Ph.D. dissertation. Gainesville, Florida: University of Florida.
- Blaser, J. (1987) Standortliche und waldkundliche Analyse eines Eichen-Wolkenwaldes (*Quercus* spp.) der Montanstufe in Costa Rica. Ph.D. thesis. Göttingen: Georg-August Universität.
- Bongers, F., Popma, J., Meave del Castillo, J. and Carabias, J. (1988) Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* **74**, 55–80.
- Braun-Blanquet, J. (1965) *Plant sociology. The study of plant communities*. London: Hafner.
- Brown, V.K. (1992) Plant succession and life history strategy. *TREE* **7**, 143–4.
- Brown, S. and Lugo, A.E. (1990) Tropical secondary forests. *J. Trop. Ecol.* **6**, 1–32.
- Budowski, G. (1968) La influencia humana en la vegetación natural de montañas tropicales Americanas. In *The Geo-Ecology of the Mountainous Regions of the Tropical Americas* (C. Troll, ed.) pp. 157–62. Proceedings of UNESCO Symposium, Mexico, August 1–3, 1966 Colloq. Geogr. 9. Bonn.
- Burger, W. (ed.) (1971–1990) Flora costaricensis. *Fieldiana Bot.* **35** and **40**, and *Fieldiana Bot. New Ser.* **13** and **23**.
- Byer, M.D. and Weaver, P.L. (1977) Early secondary succession in an elfin woodland in the Luquillo Mountains of Puerto Rico. *Biotropica* **9**, 35–47.
- Castillo, R. (1984) *Geología de Costa Rica: una sinopsis*. San José: Universidad de Costa Rica.
- Cleef, A.M. and Chaverri, A. (1992) Phytogeography of the paramo flora of the Cordillera de Talamanca, Costa Rica. In *Paramo: An Andean ecosystem under human influence* (H. Balslev and J.L. Luteyn, eds) pp. 45–60. London: Academic Press.
- Denslow, J.S. (1980) Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* **46**, 18–21.
- Di Castri, F., Robertson Vernhes, J. and Younès, T. (eds) (1992) Inventorying and monitoring biodiversity. *Biol. Int.* **27** (Special Issue). Paris: IUBS-SCOPE-UNESCO.
- Ewel, J.J. (1979) Secondary forests: the tropical wood resource of the future. In *Resúmenes del Simposio Internacional sobre las Ciencias Forestales y su Contribución al Desarrollo de la América Tropical, 11–17 Oct. 1979* (M. Chavarría, ed.) pp. 53–60. San José: CONICIT.

- Ewel, J.J. (1980) Tropical succession: manifold routes to maturity. Special issue: Tropical Succession. *Biotropica* **12** (Suppl. 2), 2–7.
- Ewel, J.J. (1983) Succession. In *Tropical rain forest ecosystems* (F.B. Golley, ed.) Ecosystems of the world 14 A, 217–23. Amsterdam: Elsevier.
- Faber-Langendoen, D. and Gentry, A.H. (1991) The structure and diversity of rain forests at Bajo Calima, Chocó region, western Colombia. *Biotropica* **23**, 2–11.
- FAO (1977) *Guidelines for soil profile descriptions*, 2nd edition. Rome: FAO.
- Gauch, H.G. (1982) *Multivariate analysis in community ecology*. Cambridge: Cambridge University Press.
- Gentry, A.H. (1982) Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann. Missouri Bot. Gard.* **69**, 557–93.
- Gentry, A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Gard.* **75**, 1–34.
- González-Espinosa, M., Quintana-Ascencio, P.F., Ramírez-Marcial, N. and Gaytán-Guzmán, P. (1991) Secondary succession in disturbed *Pinus-Quercus* forests in the highlands of Chiapas, Mexico. *J. Veg. Sci.* **2**, 351–60.
- Guevara, S., Purata, S.E. and Van der Maarel, E. (1986) The role of remnant forest trees in tropical secondary succession. *Vegetatio* **66**, 77–84.
- Hastenrath, S. (1973) On the Pleistocene glaciation of the Cordillera de Talamanca, Costa Rica. *Z. f. Gletscherk. u. Glazialgeol.* **9**, 105–21.
- Herrera, W. (1986) *Clima de Costa Rica*. San José, Costa Rica: EUNED.
- Hill, M.O. (1979a) *DECORANA—A Fortran program for Detrended Correspondence Analysis and Reciprocal Averaging*. Ithaca, New York: Department of Ecology and Systematics, Cornell University.
- Hill, M.O. (1979b) *TWINSPAN—A Fortran program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes*. Ithaca, New York: Department of Ecology and Systematics, Cornell University.
- Hill, M.O. and Gauch, H.G. (1980) Detrended correspondence analysis, an improved ordination technique. *Vegetatio* **42**, 47–58.
- Horn, S.P. (1989) Postfire vegetation development in the Costa Rican páramos. *Madroño* **36**, 93–114.
- Horn, S.P. (1990) Vegetation recovery after the 1976 páramo fire in the Chirripó National Park, Costa Rica. *Rev. Biol. Trop.* **38**, 267–75.
- IMN (1988) *Catastro de las series de precipitaciones medidas en Costa Rica*. Instituto Meteorológico Nacional. San José, Costa Rica: MIRENEM.
- Janzen, D.H. (1973) Rate of regeneration after a tropical high-elevation fire. *Biotropica* **5**(2), 111–6.
- Jiménez, W., Chaverri, A., Miranda, R. and Rojas, I. (1988) Aproximaciones silviculturales al manejo de un robleal (*Quercus* spp.) en San Gerardo de Dota, Costa Rica. *Turrialba* **38**, 208–14.
- Jongman, R.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R. (eds) (1987) *Data analysis in community and landscape ecology*. Wageningen: Pudoc.
- Kappelle, M. (1992) Structural and floristic differences between wet Atlantic and moist Pacific montane *Myrsine-Quercus* forests in Costa Rica. In *Páramo: An Andean ecosystem under human influence* (H. Balslev and J.L. Luteyn, eds) pp. 61–70. London: Academic Press.
- Kappelle, M. (1993) Recovery following clearing of an upper montane *Quercus* forest in Costa Rica. *Rev. Biol. Trop.* **41**, 47–56.
- Kappelle, M., Cleef, A.M. and Chaverri, A. (1989) Phytosociology of montane *Chusquea-Quercus* forests, Cordillera de Talamanca, Costa Rica. *Brenesia* **32**, 73–105.
- Kappelle, M., Zamora, N. and Flores, T. (1991) Flora leñosa de la zona alta (2000–3819 m) de la Cordillera de Talamanca, Costa Rica. *Brenesia* **34**, 121–44.

- Kappelle, M., Cleef, A.M. and Chaverri, A. (1992) Phytogeography of the Talamanca montane *Quercus* forest flora, Costa Rica. *J. Biogeogr.* **19**, 299–315.
- Kappelle, M., Van Velzen, H.P. and Wijtzes, W.H. (In press). Plant communities of montane secondary vegetation in the Cordillera de Talamanca, Costa Rica. *Phytocoenologia*.
- Kennis, P.A.F. and De Vries, R.A.J. (1993) Trends in diversity in mature and recovering montane *Quercus* forests, Cordillera de Talamanca, Costa Rica. M. Sc. thesis. Int. report 289. Amsterdam-Nijmegen: Amsterdam University and Nijmegen Catholic University.
- Kent, M. and Coker, P. (1992) *Vegetation description and analysis*. London: Belhaven Press.
- Lellinger, D.B. (1989) The ferns and fern-allies of Costa Rica, Panamá and the Chocó (Part 1: Psilotaceae through Dicksoniaceae). *Amer. Fern Soc.* **2A**, 1–364.
- Magurran, A.E. (1988) *Ecological diversity and its measurement*. London: Croom Helm.
- Monasterio, M., Sarmiento, G. and Solbrig, O.T. (eds) (1987) Comparative studies on tropical mountain ecosystems. Planning for research. Special issue. *Biol. Int.* **12**, 1–48. IUBS: Paris.
- Mueller-Dombois, D. and Ellenberg, H. (1974) *Aims and methods of vegetation ecology*. New York: Wiley.
- Orozco, L. (1991) Estudio ecológico y de estructura horizontal de seis comunidades boscosas en la Cordillera de Talamanca, Costa Rica. *Coll. Silv. y Manejo de Bosq. Nat.* **2**. Turrialba, Costa Rica: CATIE.
- Peet, R.K. (1974) The measurement of species diversity. *Ann. Rev. Ecol. Syst.* **5**, 285–307.
- Peet, R.K. and Christensen, N.L. (1988) Changes in species diversity during secondary forest succession on the North Carolina piedmont. In *Diversity and pattern in plant communities* (H.J. During, M.J.A. Werger and H.J. Willems, eds) pp. 233–45. The Hague: SPB Acad. Publ.
- Pielou, E.C. (1975) *Ecological diversity*. New York: Wiley.
- Purata, S.E. (1986a) Floristic and structural changes during old-field succession in the Mexican tropics in relation to site history and species availability. *J. Trop. Ecol.* **2**, 257–76.
- Purata, S.E. (1986b) Transect analysis as a basis for comparing stages of old-field succession in a tropical rain forest area in Mexico. *Trop. Ecol.* **27**, 103–22.
- Riswan, S., Kenworthy, J.B. and Kartawinata, K. (1985) The estimation of temporal processes in tropical rain forest: a study of primary mixed dipterocarp forest in Indonesia. *J. Trop. Ecol.* **1**, 171–82.
- Saldarriaga, J.G. (1985). Forest succession in the upper Río Negro of Colombia and Venezuela. Ph.D. dissertation. Knoxville, Tennessee: University of Tennessee.
- Saldarriaga, J.G., West, D.C., Tharp, M.L. and Uhl, C. (1988) Long-term chronosequence of forest succession in the upper Río Negro of Colombia and Venezuela. *J. Ecol.* **76**, 938–58.
- Shmida, A. and Wilson, K.M.V. (1985) Biological determinants of species diversity. *J. Biogeogr.* **12**, 1–20.
- Simpson, E.H. (1949) Measurement of diversity. *Nature* **163**, 688.
- Sokal, R.R. and Rohlf, F.J. (1981) *Biometry*. San Francisco: Freeman.
- Sørensen, T. (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Det. Kong. Danske Vidensk. Selsk. Biol. Skr.* (Copenhagen) **5**, 1–34.
- Standley, P. (1937–1938) Flora Costa Rica. *Field Mus. Nat. Hist.* **18**, (1–4: 391).
- Sugden, A.M., Tanner, E.V.J. and Kapos, V. (1985) Regeneration following clearing in a Jamaican montane rain forest: results of a ten-year study. *J. Trop. Ecol.* **1**, 329–51.
- SYSTAT, Inc. (1992) *SYSTAT: statistics, version 5*. 2nd edition. Evanston, Illinois. 724 pp.
- Taylor, L.R. (1978) Bates, Williams, Hutchinson—a variety of diversities. In *Diversity of insect faunas: 9th Symposium of the Royal Entomological Society* (L.A. Mound and N. Warloff, eds) pp. 1–18. Oxford: Blackwell.
- Toro, A.P. and Saldarriaga, J.G. (1990) Algunas características de la sucesión secundaria en campos de cultivo abandonados en Araracuara, Amazonas, Colombia. *Colombia Amazonica* **4**, 31–57.

- Tryon, R.M. and Tryon, A.F. (1982) *Ferns and allied plants, with special reference to tropical America*. New York: Springer.
- Tueller, P.T. and Platou, K.A. (1991) A plant succession gradient in a big sagebrush/grass ecosystem. *Vegetatio* **94**, 57–68.
- Uhl, C. and Clark, K. (1983) Seed ecology of selected Amazon Basin successional species emphasizing forest seed banks, seed longevity, and seed germination triggers. *Bot. Gaz.* **144**, 419–25.
- Van der Hammen, T., Mueller-Dombois, D. and Little, M.A. (eds) (1989) *Manual of methods for mountain transect studies: comparative studies of tropical mountain ecosystems*. Amsterdam: TME-IUBS, MAB-UNESCO and Amsterdam University.
- Van der Maarel, E. (1988) Vegetation dynamics: patterns in time and space. *Vegetatio* **77**, 7–19.
- Walker, L.R., Brokaw, N.V.L., Lodge, D.J. and Waide, R.B. (1991) Ecosystem, plant and animal responses to hurricanes in the Caribbean. Special issue. *Biotropica* **23(4a)**, 311–521.
- Weaver, P.L. (1986) Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. *Caribb. J. Sci.* **22**, 53–70.
- Weyl, R. (1980) *Geology of Central America*. Stuttgart: Bornträger.
- Whittaker, R.H. (1965) Dominance and diversity in land plant communities. *Science* **147**, 250–60.
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* **21**, 213–51.
- Whittaker, R.H. (1975) *Communities and ecosystems*. New York: Macmillan.
- Wilson, K.M.V. and Shmida, A. (1984) Measuring beta diversity with presence—absence data. *J. Ecol.* **72**, 1055–64.
- Wolf, J.H.D. (1993) Epiphyte communities of tropical montane rain forests in the northern Andes. II. Upper montane communities. *Phytocoenol.* **22**, 53–103.
- Woodson Jr., R.E. and Schery, R.W. (eds) (1943–1980). *Flora of Panama*. St. Louis, Missouri: Missouri Bot. Gard.

Appendix

Checklist of 176 alphabetically-ordered terrestrial vascular plant species found along a successional gradient in mature and recovering montane *Quercus* forests near 3000 m altitude, Cordillera de Talamanca, Costa Rica. Growthforms are given between brackets.

PTERIDOPHYTA. ADIANTACEAE: *Adiantum tenerum* Sw. [fern], *Eriosorus flexuosus* (Kunth) Copel. [fern], *Pityrogramma chrysoconia* (Desv.) Maxon [fern]. ASPLENIACEAE: *Asplenium castaneum* Schlecht. & Cham. [fern], *A. cuspidatum* Lam. [fern], *A. polyphyllum* Bertol. [fern], *A. serra* Langsd. & Fisch. [fern]. BLECHNACEAE: *Blechnum costaricense* (Christ.) C. Chr. [fern]. DENNSTAEDTIACEAE: *Pteridium aquilinum* (L.) Kuhn [fern]. DRYOPTERIDACEAE: *Arachniodes denticulata* (Sw.) Ching [fern], *Dryopteris wallichiana* (Sprengel) Hylander [fern], *Polystichum fournieri* A.R. Smith [fern], *P. muricatum* (L.) Fée [fern]. HYMENOPHYLLACEAE: *Hymenophyllum consanguineum* C. Morton [fern]. LOMARIOPSIDACEAE: *Elaphoglossum erinaceum* (Fée) T. Moore [fern], *E. furfuraceum* (Mett.) Christ [fern], *E. hirtum* (Sw.) C. Chr. [fern], *E. hoffmannii* (Mett. ex Kuhn) Christ [fern], *E. latifolium* (Sw.) J. Smith [fern], *E. squamipes* s.l. (Hook.) T. Moore [fern], *E. sp.* [fern]. LYCOPODIACEAE: *Lycopodium clavatum* L. [fern-ally], *L. thuyoides* H. & B. ex Willd. [fern-ally]. OPHIOGLOSSACEAE: *Botrychium virginianum* var. *mexicanum* Hk. & Gr. [fern]. POLYPODIACEAE: *Campyloneurum amphostenon* (Kunze) Fée [fern], *C. fasciale* (H. & B. ex Willd.) Presl. [fern], *Grammitis meridensis* (Klotzsch) Seymour [fern], *G. moniliformis* (Sw.) Proctor [fern], *Pleopeltis macrocarpa* (Willd.) Kaulf. [fern], *Polypodium loriceum* L. [fern], *P. macrolepis* Maxon [fern], *P. myriolepis* Christ [fern], *P. plebejum* Cham. & Schlecht. [fern], *P. sp.* [fern]. THELYPTERIDACEAE: *Thelypteris gomeziana* Smith & Lell. [fern]. VITTARIACEAE: *Vittaria graminifolia* Kaulf. [fern].

DICOTYLEDONES. ACTINIDIACEAE: *Saurauia veraguasensis* Seemann [tree]. APIACEAE: *Hydrocotyle bowlesoides* Math. & Const. [herb], *H. ribifolia* Rose & Standley [climber].

AQUIFOLIACEAE: *Ilex discolor* var. *lamprophylla* (Standley) Edw. [tree], *I. pallida* Standley [tree]. ARALIACEAE: *Oreopanax capitatus* (Jacq.) Decne. & Planch. [tree], *O. nubigenus* Standley [tree], *O. xalapense* (Kunth) Decne. & Planch. [tree], *Schefflera rodriguesiana* Frodin [tree]. ASCLEPIADACEAE: *Cynanchum glaberrimum* (Woods.) L.O.Wms. [climber]. ASTERACEAE: *Ageratina kupperi* (Suesseng.) King & Robinson [shrub], *A. subcordata* (Benth.) King & Robinson [shrub], *Bidens reptans* (L.) G. Don [climber], *Cirsium subcoriaceum* (Less.) Petrak. [herb], *Conyza bonariensis* (L.) Cronq. [herb], *Erigeron karwinskianus* DC. [herb], *Gnaphalium attenuatum* DC. [herb], *Jungia ferruginea* L.f. [climber], *Mikania cordifolia* (L.f.) Willd. [climber], *M. iltisii* King & Robinson [climber], *M. sp.* [climber], *Neomirandea angularis* (Robinson) King & Robinson [climber], *Roldana heterogama* (Hem.) Robinson & Brettel [herb], *R. scandens* Poveda & Kappelle [shrub], *Senecio cooperi* Greenman [shrub], *S. copeyensis* Greenman [tree], *S. multivenius* Benth. [tree], *S. oerstedianus* Benth. [herb], *Sigesbeckia jorullensis* Kunth [herb], *Verbesina oerstediana* Benth. [tree]. BEGONIACEAE: *Begonia udisilvestris* C. DC. [herb]. BORAGINACEAE: *Myosotis* sp. [herb]. BRASSICACEAE: *Cardamine bradei* O.E. Schultze [herb], *Romanschulzia costaricensis* (Standley) Rollins [herb]. CAMPANULACEAE: *Centropogon costaricae* (Vatke) McVaugh [herb], *C. gutierrezii* (Planch. & Oersted) Wimmer [herb], *G. irazuensis* Wilbur [herb], *Lobelia xalapensis* Kunth [herb]. CAPRIFOLIACEAE: *Viburnum costaricanum* (Oersted) Hemsley [tree]. CARYOPHYLLACEAE: *Arenaria lanuginosa* (Mich.) Rohrb. in Mart. [herb], *Stellaria irazuensis* Donn. Smith [herb], *S. ovata* Willd. ex Schlecht. [herb]. CHLORANTHACEAE: *Hedyosmum mexicanum* Cordemoy [tree]. CLUSIACEAE: *Clusia palmana* Standley [tree]. CORNACEAE: *Cornus disciflora* Mociño & Sessé [tree]. CUNONIACEAE: *Weinmannia pinnata* L. [tree]. ERICACEAE: *Cavendishia bracteata* (R. & P. ex St. Hil.) Hoer. [shrub], *Comarostaphylis arbutoides* Lindl. [tree], *Macleania rupestris* (Kunth) A.C. Smith [shrub], *Pernettya prostrata* (Cav.) DC. [shrub], *Thibaudia costaricensis* Klotzsch [shrub], *Vaccinium consanguineum* Klotzsch [tree]. ESCALLONIACEAE: *Escallonia myrtilloides* L.f. var. *patens* [tree]. FAGACEAE: *Quercus copeyensis* Mueller [tree], *Q. costaricensis* Liebmann [tree]. FLACOURTIACEAE: *Abatia parviflora* Ruiz & Pavón [tree]. GARRYACEAE: *Garrya laurifolia* Hartweg ex Benth. ssp. *quichensis* (Smith) Dahling [tree]. GENTIANACEAE: *Halenia rhyacophila* C.K. Allen [herb]. GERANIACEAE: *Geranium guatemalense* Kunth [herb]. GESNERIACEAE: *Solenophora calycosa* J.D. Smith [herb]. HYDRANGEACEAE: *Hydrangea asterolasia* Diels [climber]. LAMIACEAE: *Salvia iodochroa* Briq. [herb], *S. sp.* [herb]. LAURACEAE: *Nectandra cufodontisii* (Schmidt) C.K. Allen [tree], *Ocotea calophylla* Mez [tree], *O. mollicella* (Blake) Van der Werff [tree], *O. pittieri* (Mez) Van der Werff [tree], *Persea vesticula* Standley & Steyererm. [tree]. LOGANIACEAE: *Buddleja nitida* Benth. [tree]. MAGNOLIACEAE: *Magnolia sororum* Seibert [tree]. MELASTOMATACEAE: *Miconia schnelli* Wurdack [tree], *M. tonduzii* Cogn. [tree], *M. sp.* [tree], *Monochaetum neglectum* Almeda [shrub]. MYRSINACEAE: *Ardisia compressa* Kunth [tree], *A. costaricensis* Lundell [tree], *A. glandulosomarginata* Oersted [tree], *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Sch. [tree], *M. Rellucidopunctata* Oersted [tree]. MYRTACEAE: *Myrcianthes fragrans* var. *hispidula* McVaugh [tree]. ONAGRACEAE: *Fuchsia arborescens* Sims. [tree], *F. microphylla* Kunth [shrub], *F. splendens* Zucc. [herb], *Lopezia paniculata* Seemann [shrub]. OXALIDACEAE: *Oxalis spiralis* ssp. *vulcanicola* (J.D. Smith) Lourteig [herb]. PAPAVERACEAE: *Bocconia frutescens* L. [tree]. PASSIFLORACEAE: *Passiflora membranacea* Benth. [climber], *P. mollissima* (Kunth) Bailey [climber]. PIPERACEAE: *Peperomia alpina* (Sw.) A. Dietrich [herb], *P. quadrifolia* (L.) Kunth [herb], *P. saligna* Kunth [herb], *P. tetraphylla* (G. Forst.) Hook. & Arn. [herb], *Piper bredemeyeri* Jacq. [herb]. PLANTAGINACEAE: *Plantago australis* Lam. [herb]. POLYGALACEAE: *Monnina crepinii* Chodat. [tree]. POLYGONACEAE: *Muelenbeckia tamnifolia* (Kunth) Meisn. [climber], *Rumex acetosella* L. [herb]. PYROLACEAE: *Chimaphila maculata* (L.) Pursh. [herb]. RHAMNACEAE: *Rhamnus oreodendron* L.O. Williams [tree]. ROSACEAE: *Acaena elongata* L. [shrub], *Alchemilla pascuorum* (Standley) Rothm. [herb], *A. sibbaldiifolia* Kunth [herb], *Hesperomeles heterophylla* (R. & P.) Hook. [shrub], *Lachemilla pectinata* (Kunth) Rothm. [herb], *Prunus annularis* Koehne [tree], *Rubus eriocarpus* Liebmann

[shrub]. RUBIACEAE: *Galium mexicanum* Kunth [climber], *Palicourea adusta* Standley [shrub] *P. salicifolia* Standley [shrub]. RUTACEAE: *Zanthoxylum scheryi* Lundell [tree]. SCROPHULARIACEAE: *Calceolaria trilobata* Hemsley [herb], *Castilleja talamancensis* N. Holmgren [herb], *Sibthorpia repens* (L.) Kuntze [herb]. SOLANACEAE: *Cestrum irazuense* Kuntze [tree], *Solanum costaricense* Heiser [shrub], *S. dotanum* C. Morton [shrub], *S. incomptum* Bitter [shrub], *S. storkii* C. Morton [tree], *S. sp.* [herb]. STYRACACEAE: *Styrax argenteus* Presler [tree]. SYMPLOCACEAE: *Symplocos austinsmithii* Standley [tree], *S. irazuensis* Cuf. [tree], *S. serrulata* Kunth [tree]. THEACEAE: *Cleyera theaeoides* (Swartz) Choisy [tree]. TROPAEOLACEAE: *Tropaeolum emarginatum* Turcz. [climber]. URTICACEAE: *Pilea gracilipes* Killip [herb]. VALERIANACEAE: *Valeriana scandens* L. [herb]. VIOLACEAE: *Viola nannei* Polak [herb]. WINTERACEAE: *Drimys granadensis* L.f. [tree].

MONOCOTYLEDONES. ALSTROEMERIACEAE: *Bomarea acutifolia* (Link & Otto) Herb. [climber]. ARACEAE: *Anthurium concinatum* Schott. [herb]. BROMELIACEAE: *Vriesea williamsii* L.B. Smith [herb]. CYPERACEAE: *Carex jamesonii* Boot [herb], *Rhynchospora aristata* Boeckeler [herb], *Uncinia hamata* (Sw.) Urban [herb]. LILIACEAE: *Maianthemum paniculatum* (Mart. & Gal.) La Frankie [herb]. ORCHIDACEAE: *Malaxis hastilabia* (Rchb.f.) Kuntze [herb], *Spiranthes* sp. [herb]. POACEAE: *Chusquea tomentosa* Widmer & L.G. Clark [bamboo]. SMILACACEAE: *Smilax kunthii* Killip & Morton [climber].