

17 Changes in Diversity and Structure Along a Successional Gradient in a Costa Rican Montane Oak Forest

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17.1 Introduction

Tropical montane forests are among the most fragile of all ecosystems on Earth (Stadtmüller 1987; Hamilton et al. 1995; Kappelle and Brown 2001; Schneider et al. 2003). Following clearing, they recover extremely slowly, and it may take one to several centuries before their structure, composition, and function return to the original, pre-disturbance state (Ewel 1980; Hooftman 1998; Kappelle 2004). Southern temperate *Nothofagus* forest (González et al. 2002) and neotropical montane *Quercus* forests (Kappelle et al. 1994, 1995b, 1996; Ramírez-Marcial et al. 2001; Chaps. 14 and 16) appear to be no exception to this rule. To gain a deeper insight into the patterns and processes of forest recovery and resilience in Central American montane oak forests, we studied changes in structure and diversity in a series of successional vegetation patches along a time sequence, ranging from grazed and recently abandoned pastures to late-successional (35 years old) and old-growth (>200 years old) oak forest stands in the highlands of southern Costa Rica.

17.2 Study Area

The presented research on changes in vegetation structure and diversity along a successional gradient was conducted in the montane oak forest belt (2,000–3,000 m elevation) of the Cordillera de Talamanca in southern–central Costa Rica. Most sample plots were located along the Pacific slope of the largely deforested Los Santos Forest Reserve (Kappelle and Juárez 1995; Helmer 2000; Helmer et al. 2000), and on the Atlantic slope of the almost completely intact Tapantí–Macizo de la Muerte National Park. Plots are concen-

trated in the highland area between the villages of El Empalme to the northwest and Villa Mills to the southeast, both situated along the Panamerican Highway. The Tapantí–Macizo de la Muerte National Park is part of the 612,600-ha La Amistad Biosphere Reserve (a World Heritage Site), and the 62,000-ha Los Santos Forest Reserve serves as a buffer zone at the southwestern tip of the magnificent La Amistad Reserve, recognized for its amazing biodiversity by the UNESCO (Kappelle and Juárez 1994).

The Cordillera de Talamanca is made up of intrusive and Tertiary volcanic rocks alternated with marine sediments (Castillo 1984). Pleistocene glaciations have left their traces on peaks over 3,000 m (Horn 1990; Kappelle and Horn 2005). Soils are dark to pale brown, medium-textured, moderately fertile (Vasquez 1983), and very acid, with pH values of 4.5–6.5; andosols are common (van Uffelen 1991; Chap. 4). The climate is humid to super-humid, temperate to cold, and has a short dry season (January–April). The average annual temperature ranges from 10 °C at 3,000 m to about 14 °C at 2,000 m elevation (Herrera 1986). However, due to the diurnal climate reigning on tropical mountains, temperatures measured over 24 h may vary greatly, shifting from a maximum of 20–24 °C at noon to a minimum of 2–6 °C at night (Kappelle 1996; Chap. 4). Mean annual rainfall oscillates around 2,700 mm per year. Diurnal fog during most afternoons throughout the year turns the prevailing evergreen oak-dominated rainforest (1,800–3,100 m) into a true tropical montane cloud forest (TMCF; Kappelle 1992).

17.3 Plant Species Assemblages and Diversity

17.3.1 Classification of Successional Plant Communities

To date, at least 24 plant species communities have been identified in fragmented montane oak forest environments in Costa Rica's high Talamanca Range. Twelve communities correspond to mature old-growth forest (Kappelle et al. 1995a, 1989; Chap. 4), whereas another set of 12 are secondary plant communities growing at previously deforested sites (Kappelle et al. 1994, 1995b). The latter include six lower montane and six upper montane communities, with three grassland communities (grazed and recently abandoned, non-grazed pastures), one scrub association, and two 30–35 year old secondary forest types per altitudinal belt. Communities were classified on the basis of multivariate analysis of aerial crown cover data, estimated as proportions of plot area *sensu* Braun-Blanquet (1965) for terrestrial vascular plant species, and applying TWINSPLAN classification software (Hill 1979a; Kent and Coker 1992). This multivariate analysis included over 120 plant sociological, randomly stratified sample plots (sizes: 0.005–0.1 ha), located at

2,000–3,400 m elevation in the western sector of the Cordillera de Talamanca, and previously identified on aerial photographs (scale 1:60,000, year 1992, stored at the Instituto Geográfico Nacional (IGN) archives).

The twelve successional plant communities were classified as a *Monochaetum neglectum*–*Rubus eriocarpus* vegetation complex (Kappelle et al. 1994). Grasslands were characterized and dominated by species such as *Ageratina subcordata*, *Bromus* sp., *Carex jamesonii*, *Cheilanthes notholaenoides*, *Geranium guatemalense*, *Gnaphalium americanum*, *Halenia rhyacophylla*, *Holcus lanatus*, *Lolium perenne*, *Muehlenbeckia tamnifolia*, *Oenothera epilobifolia*, *Orthrosanthus chimborasensis*, *Pennisetum clandestinum*, *Plantago australis*, *Rumex acetosella*, and *Thelypteris rudis*. Diagnostic species in shrubby scrublands – locally known as ‘charrales’ – were *Galium mexicanum*, *Polypodium macrolepis*, *Pteridium aquilinum* (bracken fern) and *Vaccinium consanguineum*. Secondary forest associations were characterized by *Abatia parviflora*, *Bocconia frutescens*, *Buddleja nitida*, *Chusquea tomentosa*, *Cornus disciflora*, *Freziera candicans*, *Fuchsia arborescens*, *Monnina crepinii*, *Oreopanax xalapensis*, *Quercus copeyensis* (now known as *Q. bumelioides* – K.C. Nixon, personal communication; Chap. 1), *Q. costaricensis*, *Q. seemannii*, *Verbesina oerstediana*, *Viburnum costaricanum*, *Weinmannia pinnata* and *Wercklea lutea* (van Velzen et al. 1993; Kappelle et al. 1994).

17.3.2 Ordination of Successional Plant Communities

We applied detrended correspondence analysis (DCA) to the plant sociological data for 12 0.1-ha plots along the successional sere, using the DECORANA software (Hill 1979b; Jongman et al. 1987). This multivariate analysis revealed the occurrence of five ecological species groups arranged along the time gradient (DCA axis 1): pioneer species, early-successional secondary species, late-successional secondary species, early-recovering old-growth species, and late-recovering old-growth species (Kappelle et al. 1995b). The second axis (DCA axis 2) correlated to a moisture gradient, with species such as *Jungia ferruginea*, *Hydrocotyle bowlesiioides*, *Piper bredemeyeri*, *Senecio copeyensis* and *Solanum incomptum* inhabiting wetter sites.

17.3.3 Alpha Diversity

Along the successional gradient, a total of 176 vascular plant species in 122 genera and 75 families was identified (Kappelle et al. 1995b). Species were distributed over 52 trees, 19 shrubs, 52 herbs, 16 climbers, one bamboo, 34 ferns and two lycopods. The most speciose families were Asteraceae (20 species), followed by Polypodiaceae (10), Lomariopsidaceae (7), Rosaceae (7), Ericaceae (6), Solanaceae (6), Lauraceae (5), Myrsinaceae (5) and Piperaceae (5).

Surprisingly, terrestrial vascular species richness and density decreased with successional progress (Table 17.1). This may be due to the downslope migration of a number of herbaceous plant species that are common in the upslope subalpine and alpine paramo grassland environment (3,100–3,820 m), and invade deforested and early-successional montane habitats at lower elevation (2,300–3,100 m). Thus, alpha diversity measured using the Shannon-Wiener index (H' ; see Magurran 1988) appeared to be far higher in secondary forests than in old-growth mature forest, for the 12 0.1-ha plots at 2,800–3,000 m. In fact, the Shannon-Wiener index for terrestrial vascular plant species dropped significantly (Tukey-Kramer's one-way ANOVA test, $p < 0.05$) from 5.1 in early-successional forest to values below 4.5 in mature, old-growth forest (Kappelle et al. 1995b). Probably, in mature old-growth forest, larger plot sizes are needed to ensure that most of the terrestrial plant species are included in the analysis. Shannon-Wiener's diversity index was also calculated, for tree species only (42 species). The index values fluctuated in the range 2.9–3.9 but did not change significantly along the gradient (Student's t test, $p > 0.02$; Kappelle et al. 1996).

17.3.4 Beta Diversity and the Minimum Time for Floristic Recovery

We were able to calculate beta diversity on the basis of a chronosequence of successional and old-growth montane oak forest plots (Fig. 17.1). Beta diversity analysis helped us to estimate the minimum time required for a previously forested but now cleared and abandoned site to recover to acceptable levels in terms of plant species composition and diversity. Acceptable levels are defined as those at which the flora of a recovering site has a similarity of 95% in comparison with the original flora of a non-cleared, pristine forest site. To calculate these levels, beta diversity was assessed as the degree of similarity between pairs of successional and mature, old-growth forest stands, using Sorensen's coefficient of community (CC) or similarity coefficient (Jongman et al. 1987). Subsequently, similarity values were extrapolated in time (period of recovery since abandonment) by fitting data to a linear regression equation. Beta diversity was found to decrease along the successional gradient, and the theoretical minimum floristic recovery time – including only terrestrial vascular plants – was estimated at approximately 65 years ($r^2 = 0.66$). Thus, about a third of the total variance of Y before regression remains unexplained in this case.

Table 17.1. Stand structure and diversity data for nine 0.1-ha plots in successional montane oak forest at ~2,950 m a.s.l. in Costa Rica. Values are based on plot data presented in Kappelle et al. (1995b, 1996). Similar data for mature old-growth oak forest are presented in Chap. 10

Variable ^a	1	2	3	4	5	6	7	8	9
Stand age (years following abandonment)	8	10	12	20	20	25	30	30	32
Canopy height (m)	8	8	9	14	11	11	16	17	18
Number of stems ≥ 3 cm DBH per plot	193	167	219	325	313	229	302	216	327
Number of stems ≥ 10 cm DBH per plot	5	12	13	71	39	23	84	59	85
Number of stems per diameter class									
Stems 3–5 cm DBH per plot	123	111	137	90	132	116	104	72	141
Stems 5–10 cm DBH per plot	65	44	69	164	142	90	114	85	101
Stems 10–20 cm DBH per plot	5	11	13	65	37	22	79	49	65
Stems 20–40 cm DBH per plot	0	1	0	6	2	1	5	10	20
Stems >40 cm DBH per plot	0	0	0	0	0	0	0	0	0
Stem density (stems ≥ 3 cm DBH per ha)	1,930	1,670	2,190	3,250	3,130	2,290	3,020	2,160	3,270
Basal area for stems ≥ 3 cm DBH ($\text{m}^2 \text{ha}^{-1}$)	4.5	4.8	5.7	20.5	13.3	8.7	19.3	16.5	25.3
Species richness per plot (terr. vasc.) ^b	91	91	98	91	100	90	75	90	75
Species richness per plot (trees only)	18	21	15	21	30	18	20	19	24
Shannon-Wiener's index (terr. vasc.)	5.07	5.06	5.19	5.39	5.39	5.20	4.73	4.63	4.74
Shannon-Wiener's index (trees only)	3.32	3.23	2.96	3.56	3.90	3.47	2.92	3.29	2.90
Reciprocal Simpson's index (terr. vasc.)	17.2	15.5	11.2	24.4	22.4	17.7	11.7	7.9	6.3
Reciprocal Simpson's index (trees only)	6.90	5.41	5.68	9.62	9.26	8.39	3.88	5.39	3.92
Species density (terr. vasc.)	30.3	30.3	32.6	30.3	33.3	30.0	25.0	30.0	25.0
Evenness or equitability index (terr. vasc.)	0.78	0.78	0.78	0.83	0.81	0.80	0.76	0.71	0.76

^aShannon-Wiener's index, reciprocal Simpson's index, species density, and evenness index were measured following procedures presented in Magurran (1988)

^bTerr. vasc., all terrestrial vascular plant species

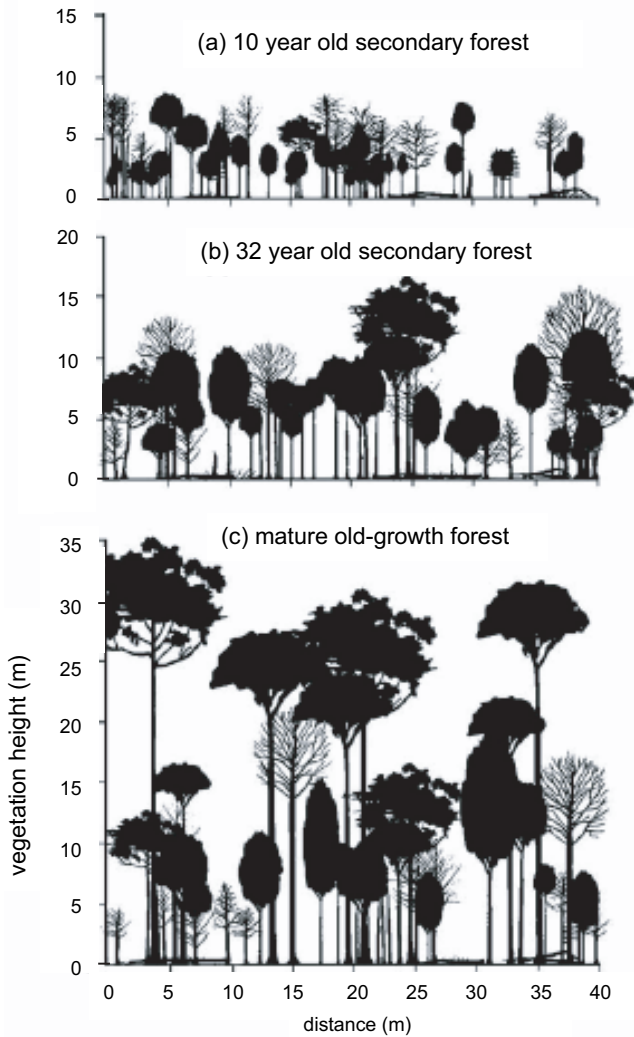


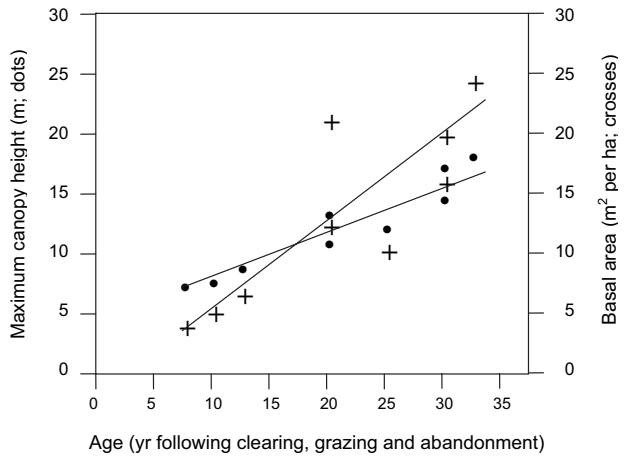
Fig. 17.1a–c. Schematic lateral profiles of three successional stages of tropical montane oak-bamboo forest at 2,700–2,900 m elevation in Costa Rica (Talamanca Mountains): **a** 10-year-old successional forest following clearing, grazing and abandonment; **b** 32-year-old successional forest following clearing, grazing and abandonment; and **c** >250 year old, mature old-growth oak-bamboo forest. Reproduced from Kappelle (2004), with permission from Elsevier

17.4 Stand Structure

17.4.1 Forest Layering

The maximum height of the closed forest canopy varied in the range ca. 5–8 to 14 m in early-successional forest, 11–18 m in late-successional forest, and 35–40 m in mature old-growth forest (Fig. 17.2; Kappelle et al. 1996; Chap. 10). Only mature old-growth forest stands showed stratification into two horizontal tree layers: a 20–40 m tall, uniform canopy layer dominated by oak, and a

Fig. 17.2. Maximum canopy height (dots) and basal area (crosses) as functions of time of recovery following old-growth forest clearing, grazing and abandonment at nine 0.1-ha, 8–32 year old successional forest plots in San Gerardo de Dota, Costa Rica. Lines are drawn using coefficients of linear regressions for both functions



3–20 m tall, mixed subcanopy layer with species belonging to *Ardisia*, *Cleyera*, *Myrsine*, *Ocotea*, *Schefflera*, *Styrax*, *Vaccinium* and *Weinmannia*, together with younger and smaller oaks.

17.4.2 Stem Density and Basal Area

In all 2,854 stems ≥ 3.0 cm DBH (diameter at breast height) were counted, identified, and measured in 1.2 ha of successional and old-growth forest stands (Kappelle et al. 1996; Table 17.1). Numbers of stems decreased with increasing stem diameter for all successional forest phases. The proportion of tree stems ≥ 10.0 cm DBH increased from 3% in late-successional forest to 40% in mature, old-growth forest. Stem density fluctuated between 1,670 stems per ha in 10-year-old early-successional forest and 3,270 stems per ha in 30–35 year old, late-successional forest. Stem density was significantly higher in late-successional forest than in mature, old-growth forest (Student's *t* test, $p < 0.05$). Basal area increased linearly with plot age for successional forest stands, and ranged from 4.46 m² per ha in 8-year-old early-successional forest to 64.69 m² per ha in mature, old-growth forest (Kappelle et al. 1996). Basal area increased during succession (Fig. 17.2), and was significantly higher in mature, old-growth forest than in early- or late-successional forest (Student's *t* test, $p < 0.001$).

17.4.3 Growth and the Minimum Time for Structural Recovery

Forest canopy height and DBH are significantly correlated for stems ≥ 3.0 cm DBH occurring along the assessed successional gradient (logarithmic regres-

sion, $r^2=0.72-0.92$, $p<0.001$). Similarly, for successional forest stands, forest canopy height, basal area and recovery time (plot age) revealed significant linear regressions ($r^2=0.68-0.97$, $p<0.001$). On the basis of the latter regression equation, the theoretical minimum time needed for forest recovery was estimated (1) by solving for X (age) where Y (canopy height) is the mean old-growth forest canopy height of 36 m, in which case the minimum time required for a successional forest to reach structural maturity was estimated at 79.5 years; and (2) by solving for X (age) where Y (basal area) is the mean old-growth forest basal area of 60.3 m² per ha, in which case the minimum time required for a successional forest to reach structural maturity was estimated at 89.0 years (Kappelle et al. 1996). In both cases, structural maturity does not account for the presence and abundance of epiphytes. To synthesize, an average recovery period of 84.3 years ($r^2=0.68-0.86$) can be calculated for a successional montane oak forest to become structurally similar to old-growth forest – excluding epiphytic richness and biomass, which may take many more decades to recover fully (Chaps. 7 and 21). Still, 15–35% of the total variance of Y before these regressions remains unexplained.

17.5 Conclusions

An important trend that has been noted in this study is the significant decrease in vascular plant diversity as secondary succession advances. The outcomes of the diversity measures substantiate this trend, and confirm results from earlier research in the same study area that focused on tree species recovery (Kappelle 1993), ground cover recuperation (A. Schumacher, personal communication), and vascular plant recovery at the forest–pasture edge (Oosterhoorn and Kappelle 2000). These outcomes are concordant with the hypothesis that high species diversity in successional forests is commonly due to a high degree of vertical and horizontal micro-environmental heterogeneity (high niche differentiation) in young recovering forest (Bazzaz 1975).

Another explanation is provided by the theory that a large number of plant species naturally found in upslope, subalpine and alpine vegetation communities may disperse downslope into successional patches – a process locally known as ‘paramization’ (Kappelle and Horn 2005). Examples of these light-demanding species are the trees *Abatia parviflora*, *Buddleja nitida*, *Comarostaphylis arbutoides*, *Escallonia myrtilloides*, *Fuchsia arborescens*, *Garrya laurifolia* and *Verbesina oerstediana* – all very abundant in subalpine paramo communities at 3,200–3,400 m elevation (Kappelle et al. 1991). These species are all adapted to open, harsh environments, and apparently provide more favorable conditions at microsites for the establishment of shade-tolerant, late-successional and typical mature oak forest genera such as *Chusquea*, *Cleyera*, *Quercus*, *Vaccinium*, *Weinmannia*, and oak. As canopy closure

occurs, these latter species may outcompete the light-demanding species of subalpine and alpine origin.

Finally, a third explanation for the high number of species in early phases, compared to old-growth forest, is provided by Denslow (1980). She suggests that species diversity in successional phases in tropical forests is initially high due to the high number of seedlings of possibly disturbance-adapted – in our case, subalpine and alpine – species in the early stages of recovery. Availability, dispersal, and germination of seeds of such species may indeed play a key role in speeding up forest recovery during initial stages at cleared sites (Chaps. 18, 23, 24 and 25).

Oak species commonly show high recovery capacity (e.g., Chaps. 13, 18 and 22). After clearing, burning, grazing, and subsequent abandonment, oaks with stems ≥ 3 cm DBH appear in 8–10 year old, early-successional forest. As soon as acorn germination and establishment have been successfully completed, stem numbers of oak increase rapidly throughout the first successional stages. After 30–35 years stem density levels off, whereas stem size continues to increase and reaches highest values at the end of the successional pathway – when the tree falls, causing a gap and initiating a renewed phase of local forest-interior recovery (gap dynamics). When forest maturity has been reached, the distribution of oak stems (in numbers) based on DBH size class displays an inverted J-shaped curve – a model previously observed in other parts of the Talamancan montane oak forests (Jiménez et al. 1988).

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