Chapter 32
Succession Stages of Vegetation Regeneration: Secondary Tropical Mountain Forests

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32.1 Introduction

Successional stages of a vegetation development leading from bare soil to a plant cover dominated by bushes and a few pioneer trees have been described by Beck et al. (see Chapter 27 in this volume). Under optimal conditions this succession continues to a secondary mountain forest, the analysis of which proves to be an enormous challenge, not only from a scientific but also from a logistic viewpoint. Tropical secondary mountain rain forests appear to be the most difficult vegetation type for a systematic investigation.

In the RBSF at least three types of secondary forest can be differentiated: Forest coming up on clear-felled areas, forests regenerating on mud-flows, and forest recovering from a fire. As these forests are almost impenetrable thickets, a complete inventory of their plant diversity is hardly achievable and therefore additional structural analysis is indispensable.

Seven patches of secondary forests, covering areas of between 1500 m^2 and 2200 m^2 in a narrow altitudinal range between 1950 m and 2100 m were investigated. Four of these (C1–C4) represent regeneration stages from small-sized clearings during the 1950s and 1960s for the construction/reconstruction of a water pipeline to the nearby power plant. They were found alongside the Camino Canal, where they border the primary forest. One plot (L) developed on the accumulated material of a mudflow, and two (F1, F2) are forests in a Quebrada which are recovering from a fire, as witnessed by several charred trunks. F1 and F2 are flanked by pastures or bracken fields.

As the climatologically conditions of these seven forests are similar, the differences shown below must result from their different ages and from the different modes of disturbance of the original forest.

E. Beck et al. (eds.), *Gradients in a Tropical Mountain Ecosystem of Ecaudor. Ecological Studies 198.*

32.2 Methods

The seven plots were subdivided into 5 × 5 m subplots which were then individually analyzed for species composition. Species were identified using mainly the *Flora of Ecuador* (Harling and Andersson 1973–2003) and the *Herbarium Reinaldo Espinosa* (Universidad Nacional de Loja). Although rough estimates on the cover abundances of the individual plant species were made, Jaccard distance indices were calculated based on presence/absence data. Further, the nonlinear ordination technique “isometric feature mapping (Isomap)” (Tenenbaum et al. 2000) was used for a low-dimensional projection of the data set. The methodological details are described in detail by Mahecha et al. (2007), including a broad methodological comparison of different ordination techniques.

32.3 Results and Discussion

In total about 770 vascular plant species were recorded, half of which could be reliably identified to genus, but only 20% to species; and 8% could not be identified. New species and species new for southern Ecuador were recorded. No minimum area could be established for any one of these forests, which is typical of tropical

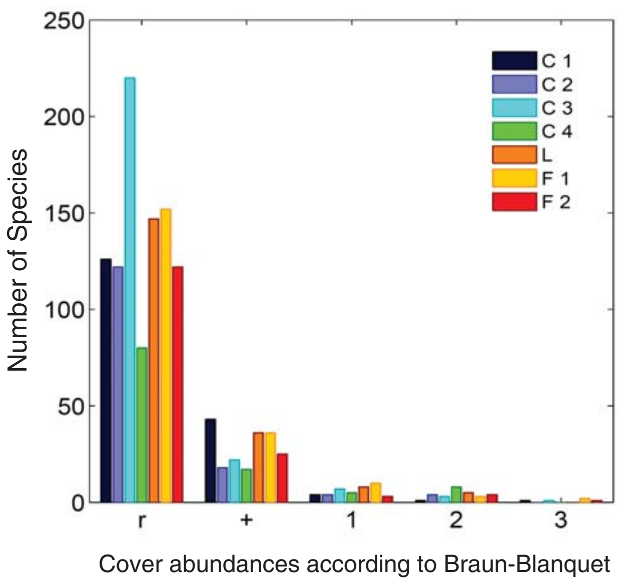

Fig. 32.1 α-Diversity (frequency) and cover abundances of the species recorded in the seven plots of secondary forest

secondary forests. The inventory of the vascular plants shows the extraordinary diversity and the concomitant low cover abundances of the individual species (Fig. 32.1). Another typical feature of secondary tropical forests is the heterogeneity of species distribution, reflected by a high degree of local species turnover. Assessing spatial heterogeneity in terms of β-diversity is crucial for understanding the succession development of secondary tropical forests. Figure 32.2 gives an impression

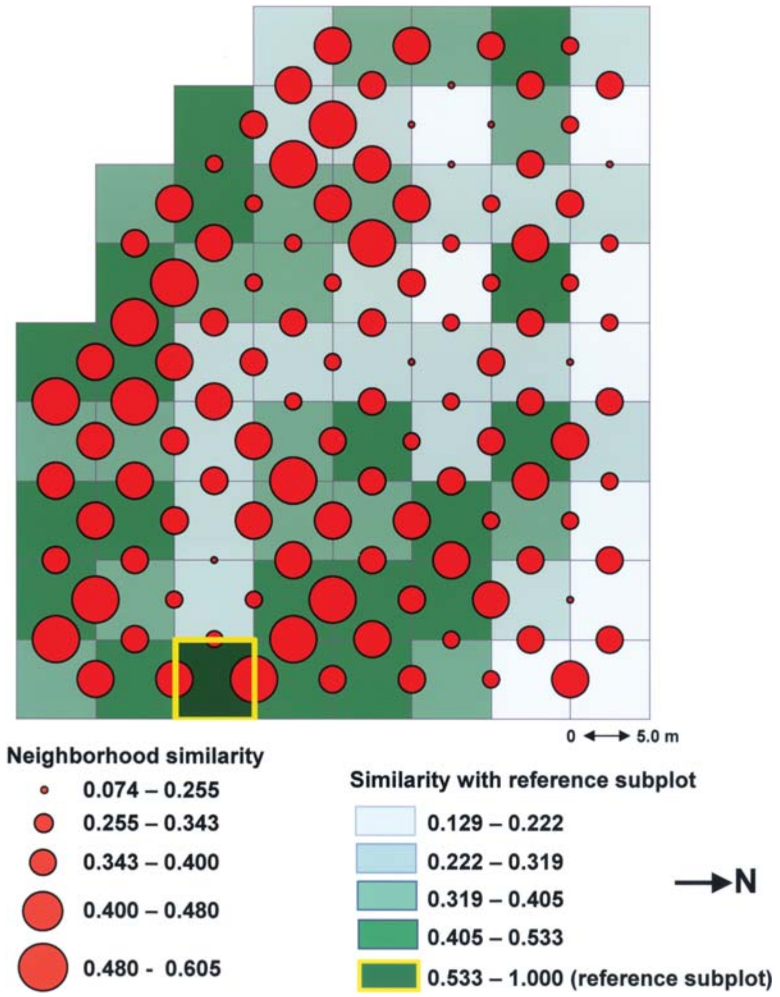

Fig. 32.2 Neighborhood similarity of subplots of Plot C4 based on the Soerensen indices. The colors of the quadrangular subplots indicate the similarity of each subplot with the reference subplot (indicated by the yellow frame), while the circles show the similarity of adjacent plots. Plot C4 is the oldest successional stage of the investigated series

of the heterogeneity of species occurrences at C4. Both the dissimilarity compared with a reference grid cell and the similarity of neighboring spatial plots show the heterogeneity of that patch of secondary forest.

Investigating the relationships between the respective plots requires methods of dimensionality reduction, well known as ordinations (Legendre and Legendre 1998). It was soon recognized that conventional linear ordination methods were not able to capture the inherent patterns of the species inventories, which require depicting not only a high α-diversity, but also high degrees of β-diversity (Williamson 1978; Bradfield and Kenkel 1987; Dea'th 1999). Recently, Mahecha and Schmidtlein (2007) showed that such problems can be overcome by nonlinear ordinations (such as Isomap) by emphasizing the spatial species turnovers only. Indeed, Isomap extracted a well interpretable ordination space comprising the individual plots in one data set (Fig. 32.3a), which explained 78% of the data variance. This ordination further allowed a common visualization of α- and β-diversity (Fig. 32.3b; Mahecha et al. 2007). In that ordination space the series C1–C4 shows, in a space-for-time sequence, the succession on areas where fire played no or only a minor role in forest clearing. Forests C2 and C3 border on the Camino Canal in a horizontal distance of 700 m and their age is about 45 years (C2) and 50 years (C3). Although both forests expectedly share a higher degree of similarity, they are clearly separated by the Isomap ordination. The youngest secondary forest in that series (C1; about 30 years old, which has transitorily been used as an agricultural field) and the oldest (C4; more than 60 years old) represent the corner marks of that series. The forests on plots F1 and F2 have been recovering from a fire for about 15 years and, because their areas are in close vicinity, they show a high degree of similarity. But from their floristic composition, as well as from their structure, they are clearly separated from the series C1–C4 and even more from forest "L" which has developed on a mudflow in a gully. Using the Isomap ordination technique, the peculiarities based on the different origins and ages of these heterogeneous second-

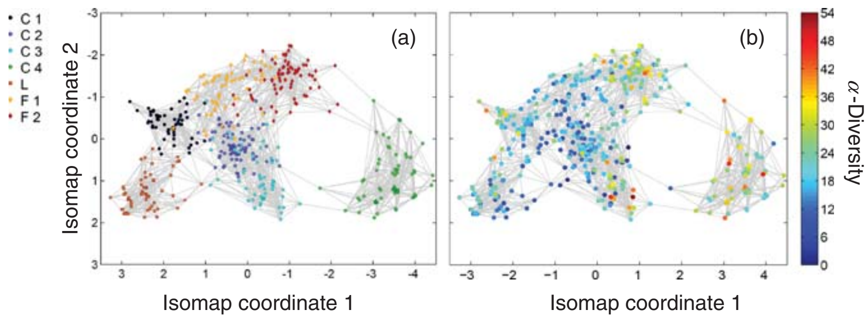

Fig. 32.3 Two-dimensional Isomap ordination based on the subplot floristic composition. Colors indicate different plots (**a**) and α-diversity (**b**), respectively. Reprinted from Mahecha et al. (2007), with permission from Elsevier

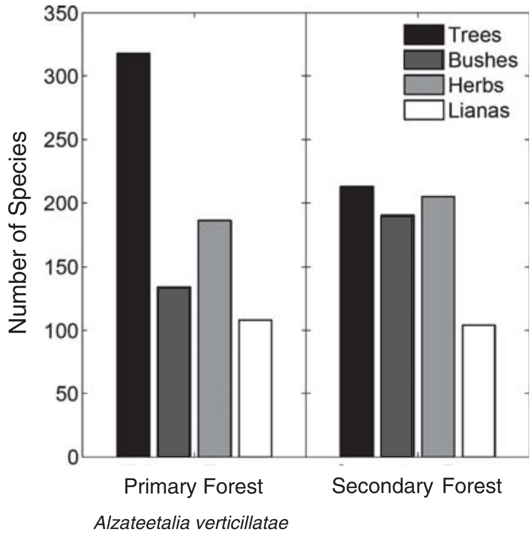

Fig. 32.4 Proportions of the various plant life forms of secondary and primary forest of the RBSF. The plant community "*Alzateetalia verticillatae*" was described by Bussmann (2002) as a formation of the primary lower montane forest of the area

ary forests can be clearly demonstrated. For example it can be seen that the α-diversity appears as a function of the successional stage of the vegetation as reflected by an increasing species richness with time. However, similar high numbers of species were found in earlier stages of succession, depending on a different mode of disturbance, i.e. on plots affected by fire (Fig. 32.3b).

Our findings further revealed that the investigated secondary forests differ structurally from the corresponding primary forest (Bussmann 2002) by a smaller share of trees (Fig. 32.4) concomitantly with a higher proportion of bushes and tree ferns, whereas the contributions of the plant life forms herbs and lianas are rather similar. According to that composition of plant life forms the secondary forests have a less homogeneous and a more open appearance, as shown by the profiles in Fig. 32.5.

32.4 Conclusions

Floristic as well as structural analysis of a tropical secondary mountain rain forest can be performed using the classic standard Braun–Blanquet relevés and true-to-scale recordings of the transects. However, the mixture of cover and abundance scales in this kind of relevés do not allow any further statistical analysis. Additional biases are caused by highly subjective estimates of cover values in multistrata tropical mountain rain forests. Moreover, since the prerequisite of homogeneous vegetation

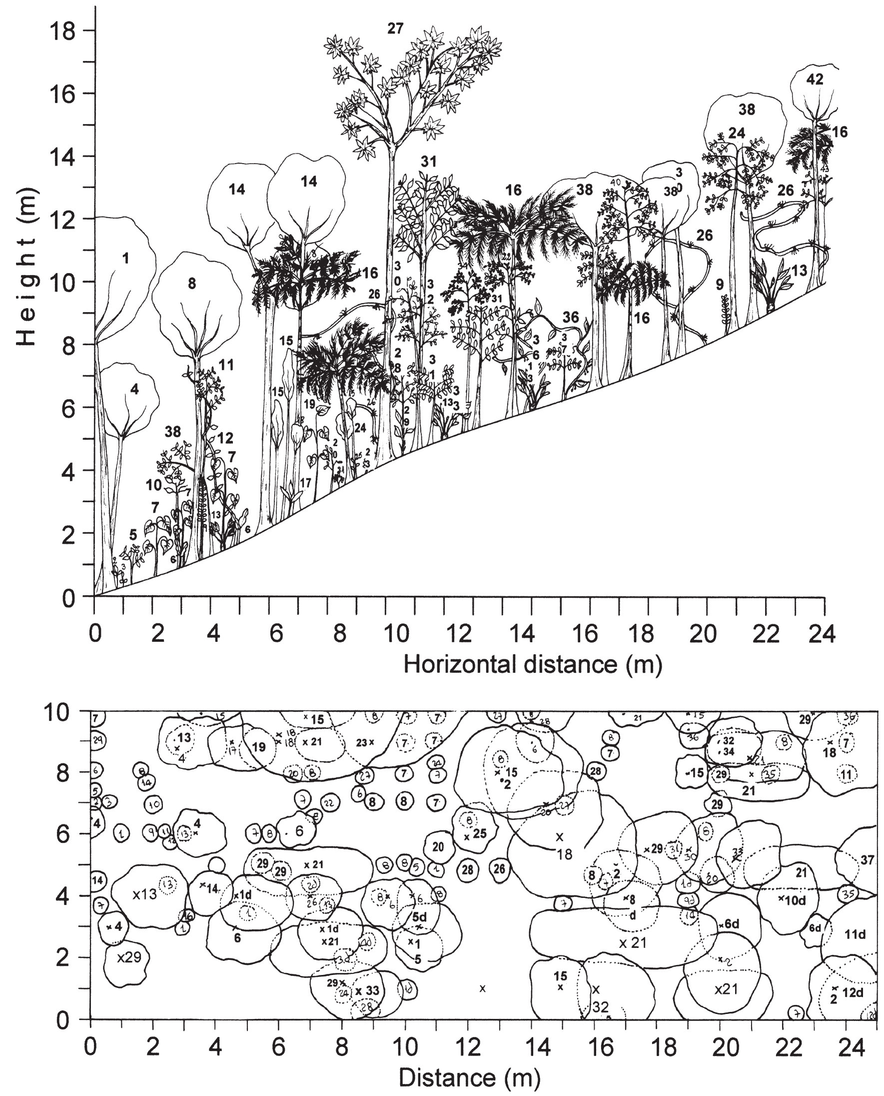

Fig. 32.5 Vertical (**a**) and horizontal (**b**) vegetation profiles of the secondary forest of plot C4 (undisturbed at least since 1962, according to the oldest aerial photograph). Explanation of the plant *numbers* given in the profiles: *1 Heliocarpus americanus*, *2 Trichilia* sp., *3 Commelina* sp., *4 Viburnum obtectum*, *5 Palicourea* sp., *6 Heliconia escarlatina*, *7 Anthurium giganteum*, *8 Persea* sp., *9 Philodendron* sp., *10 Piper parareolatum*, *11 Miconia* sp. 1, *12 Mikania* sp., *13 Asplundia* sp., *14 Inga acreana*, *15 Nectrandra* sp. 1, *16 Cyathea caracasana*, *17 Asplenium serra*, *18 Hedyosmum* sp., *19 Anthurium dombeyanum*, *20 Alchornea glandulosa*, *21 Paullinia* sp., *22 Nectandra* sp., *23 Peperomia* sp., *24 Miconia* sp. 2, *25 Hyeronima moritziana*, *26 Chusquea* sp., *27 Cecropia gabrielis*, *28 Guatteria* sp., *29 Stenospermation* sp., *30 Micropholis guyanensis*, *31 Psychotria tinctoria*, *32 Monnina* sp., *33* Lauraceae 1, *34 Tapirira guianensis*, *35* Lauraceae 2, *36 Cavendishia* sp., *37 Miconia theaezans*, *38 Hedyosmum anisodorum*, *39 Clusia* sp., *40 Matayba inelegans*, *41 Miconia* sp. 3, *42 Dendropanax* sp., *43 Myrsine coriacea*, *1d Piptocoma discolor*, *2d Miconia* sp. 4, *3d Naucleopsis glabra*, *4d Ficus* sp., *5d Parinaria* sp., *6d Trichilia* sp., *7d Wettinia equatorialis*, *8d Persea* sp. 2, *9d Guarea* sp., *10d Anthurium trisectum*

responses to environmental gradients and succession trajectories is not fulfilled, data needed for analysis are based only on the presence/absence information for species. Using the Isomap procedure a satisfactory description of the secondary forests was possible in terms of variance explanation in connection with a meaningful low dimensional visualizations of the underlying patterns of the traced succession. The simultaneous visualization of α- and β-diversity uncovered systematic patterns of vegetation development as a function of time and of the type of disturbance.