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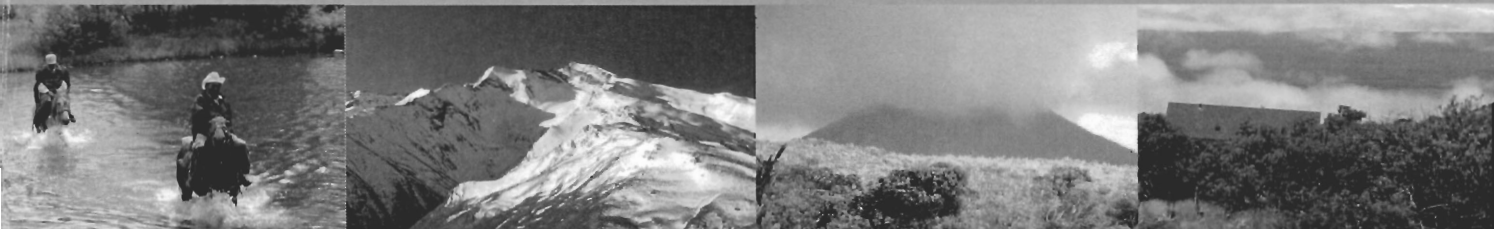# Environmental
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8 Secondary Succession in the High Tropical Andes: Monitoring in Heterogeneous Environments

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LONG FALLOW AGRICULTURE IN THE PARAMOS: AN OPPORTUNITY TO ANALYSE RESTORATION DYNAMICS IN ALPINE ENVIRONMENTS

One of the main characteristics of mountain environments is their high spatial heterogeneity, with continuous gradients of topography, exposition, slope, altitude, rain, stoniness, temperature and so on. This exceptionally high heterogeneity complicates the establishment of successional patterns using synchronic approaches. Our aim in this contribution was to use the available information on paramo old-field succession to discuss methodological and theoretical difficulties in monitoring ecological dynamics in heterogeneous environments. Some of our conclusions could be generalized with respect to other mountain regions because of their intrinsic heterogeneous nature.

In the alpine belt of the Northern Tropical Andes (paramos), between 3,000 and 3,800 m, long fallow agriculture is still practiced by semi-traditional farmers in the cultivation of potatoes and cereals. This kind of agriculture alternates periods of cultivation of two or three years with fallow periods of between five and more than ten years (Ferwerda, 1987; Sarmiento, et al., 2002). Because long fallow agriculture generates a landscape mosaic in which natural vegetation areas and plots under cultivation coexist with plots in different seral stages, it provides a unique opportunity to study the mechanisms of secondary succession after agriculture disturbance in alpine environments, including the interrelations between plant and soil processes. Several authors have studied this succession and found that the restoration of paramo vegetation in old-fields proceeds relatively fast (Ferwerda, 1987; Jaimes and Sarmiento, 2002; Sarmiento et al., 2003), contrary to the commonly held assumption that succession in alpine ecosystems is a slow process. Among the factors that probably enhance paramo restoration are the intricate mosaic nature of the landscape and the short duration of the cultivation period. These factors could facilitate the persistence of a viable seed bank and vegetation colonization into fallow fields from adjacent natural areas.

Despite the relatively fast restoration of paramo physiognomy, some characteristic paramo species do not recolonize during the first ten to fifteen years of succession. Consequently,

vegetation in advanced seral stages is less diverse than in the original paramo. Sarmiento et al. (2003) analysed plant succession in the paramo and concluded that there are clear patterns of change in species abundance. Other aspects of secondary succession, such as fertility restoration and associated changes in soil properties, have also received considerable attention. In the case of soil properties, however, trends are more difficult to establish (Ferwerda, 1987; Llambí and Sarmiento, 1998; Jaimes, 2000; Morales and Sarmiento, 2002; Sarmiento and Bottner, 2002; Abadín et al., 2002). This is probably due to the longer response time of measured soil variables and to the high environmental heterogeneity of these mountain valleys, which masks possible underlying trends.

MONITORING VEGETATION CHANGES

In order to establish some possible generalities about monitoring vegetation changes in mountain environments, some of the available data on vegetation succession in the paramo are reanalysed. The information was collected in a small glacial valley of the Venezuelan paramos (Paramo de Gavidia) where long fallow agriculture is practised between 3,300 and 3,800 m a.s.l. The vegetation of thirty-six plots that had lain fallow for different periods (one to nine years) was analysed in four consecutive years. In addition, eight areas of never-cultivated paramo (virgin paramo) were included, but sampled only once. Some of the results were published in Sarmiento et al. (2003).

Figure 8.1 presents the ordination diagram (Detrended Correspondence Analysis) of the plots according to their plant species abundance, considering the four sequential samplings of each plot. The first axis of the ordination is significantly correlated with fallow time, showing the clear directionality of the successional process. Early succession plots are on the left-hand side of the figure and virgin paramo ones on the right. Nevertheless, there is an important overlap between plots that have been fallow for different lengths of time, indicating that the rate of succession is not the same for all plots. This aspect can be illustrated by comparing trajectories B and D in the diagram, which correspond to two plots that at the beginning of the study presented similar vegetation structures. They start very close to each other in the ordination diagram, but go over very different distances along the first axis in the four-year sampling interval.

The second axis is associated with divergence (different successional pathways) between plots. For example trajectories A and C correspond to two plots that followed different pathways and consequently ended up with contrasting vegetation compositions after four years. Early succession plots are more similar to each other in plant community structure than late ones, suggesting that divergence increases as succession proceeds.

For monitoring purposes these two aspects, different rates of succession and divergence, can be very important. For example, if a synchronic analysis of succession is carried out and the selected plots experience different rates of succession, the successional sequence of changes will be masked or incorrectly established. Also, if the selected plots follow different successional pathways the comparison between them will not make it possible to establish the correct successional sequence within any of the alternative pathways. These sources of error can be reduced if a large number of plots are selected or if the synchronic analysis is complemented
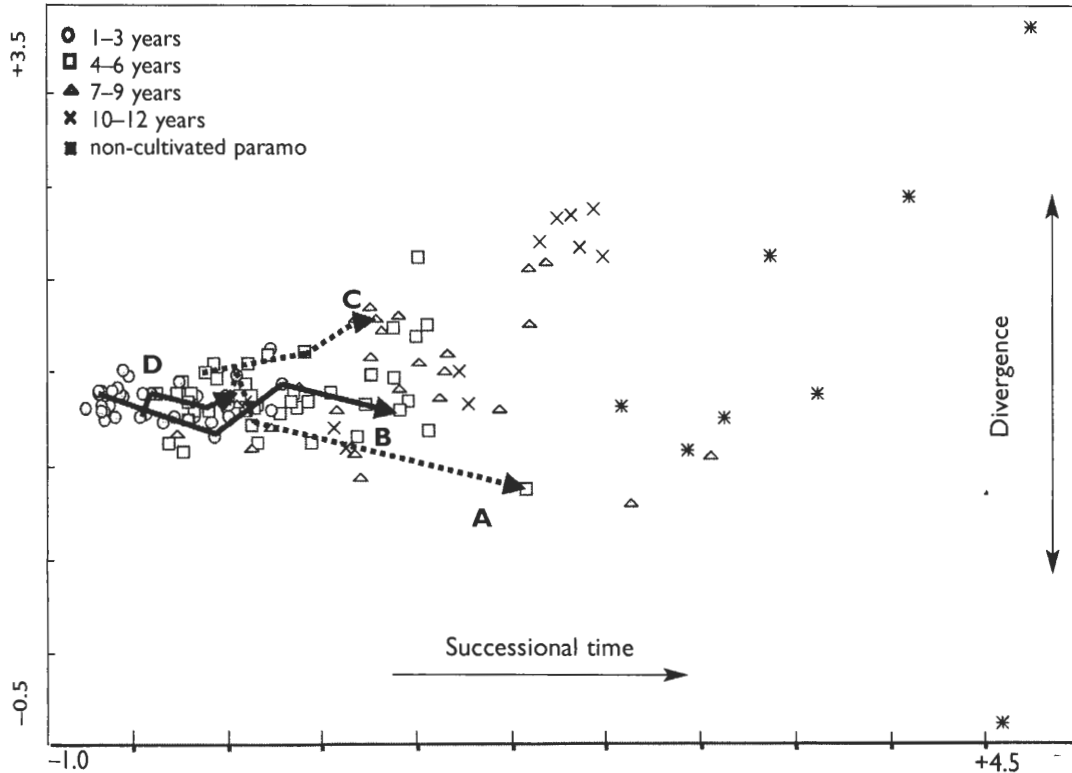
Figure 8.1

Ordination diagram using Detrended Correspondence Analysis (DCA) of species abundance in thirty-six plots with different successional age, analysed during four consecutive years (1996–1999) and eight areas of never-cultivated paramo (Paramo de Gavidia)

The arrows show the trajectories of four plots that illustrate different pathways (A and C, dashed lines) and rates of succession (B and D, solid lines).

Source: modified and complemented from Sarmiento et al (2003).

with a diachronic analysis. Efforts directed to the selection of the plots to be sampled, using homogeneity criteria, can also contribute to reducing environmental variability, allowing a more clear-cut interpretation of temporal trends.

Another aspect of secondary succession that is relevant for monitoring purposes and for the identification of ecological indicators is the behaviour of alien or introduced species during secondary succession. Sarmiento et al. (2003) and Jaimes (2000) reported that in the Venezuelan and Colombian paramos introduced species are much more abundant early in succession, declining continuously throughout the fallow period, and are rare species in the virgin paramo. These ruderal species are good indicators of disturbance. On the other hand there are many species that do not appear during the first twelve years of succession but can by found in the undisturbed paramo. The absence of these species can also be an indicator of disturbance.

Despite the different rates of regeneration and the existence of alternative successional pathways, successional patterns of changes in abundance of individual species follow clearly identifiable trends. It is possible to define several categories in terms of the species abundance at different seral stages: non-persistent pioneer species, persistent pioneers, intermediate species, late successional species, exclusive paramo species and those without any clear trend. Depending on the characteristics of each plot and its surroundings area, a particular species may or not participate in the succession. Consequently the presence of a particular species and its abundance is a much better indicator of a seral stage than its absence.

MONITORING THE EFFECT OF GRAZING ON SECONDARY SUCCESSION

Fallow plots in the paramos are subject to grazing by cattle and, to a lesser extent, by horses and sheep (Pérez, 2000; Jaimes, 2000). This kind of disturbance is likely to affect plant succession, modifying the competitive relationships between species and affecting vegetation structure and the rates and pathways of secondary succession (Davidson, 1993; Van Oene et al., 1999). This aspect was analysed in an exclusion experiment carried out between 1998 and 2001 in the Paramo de Gavidia. The results have been only partially published in Sarmiento (2004). For this experiment eight plots were selected, four in the first year the succession (young plots) and four with five years in succession (old plots). All the plots were adjacent (less than 800 m between them) and located close to the valley bottom. In each plot an area of 200 m² was fenced off. Cattle were excluded from half of this area, while the other half was grazed with a stocking rate of approximately 0.55 cows ha⁻¹. Vegetation was sampled twice a year over a four-year period.

When the effect of grazing is analysed plot by plot, clear trends can be identified. Figure 8.2 is an ordination diagram of the vegetation carried out in a young fallow plot. Both sections of the plot (grazed and ungrazed) started with the same plant community structure (the same position in the diagram) but followed different trajectories. The first ordination axis can be associated with successional time and the second axis with the grazing treatment. Pioneer species are associated with the left-hand side of the diagram and late successional species with the right-hand side. Successional time accounts for most of the vegetation changes (the trajectories followed by plant community structures are almost parallel to the first axis, which is correlated with time and accumulates the largest percentage of the total variance), but grazing produces a consistent effect, with the points corresponding to each treatment – grazed and ungrazed – being clearly separated along the second axis. Species can be classified in terms of the effect of grazing as those that are negatively affected (*Nassella mexicana, Bromus carinatum, Trisetum irazuense, Lupinus meridanus*), positively affected (*Poa annua, Penisetum clandestinum, Agrostis trichodes*) and those on which grazing has only a slight effect (such as *Paspalum lineispatha, Acaena elongata* and *Rumex acetosella*). In short, time and grazing had different but consistent effect on vegetation development in this particular plot. The same is true of all other plots when analysed separately.

However, when all the plots are analysed simultaneously, it becomes more difficult to establish consistent patterns. Figure 8.3 shows the ordination diagram of the eight plots. The first axis is correlated with time, with early successional plots appearing at the left-hand side. However, grazing is not significantly correlated with any of first four axis of variation. The individual characteristics of the plots (spatial heterogeneity) have a greater effect on vegetation structure and its temporal trajectories than grazing. In fact, when plots were classified in terms of the grazing treatment, they did not form consistent groups in the ordination diagram. Divergence between successional pathways due to the individual conditions of each plot is more important than grazing in determining vegetation structure; this complicates the analysis of the effect of grazing using replicated experiments, thus making difficult data analysis (using conventional statistical techniques) and the derivation of generally applicable rules.
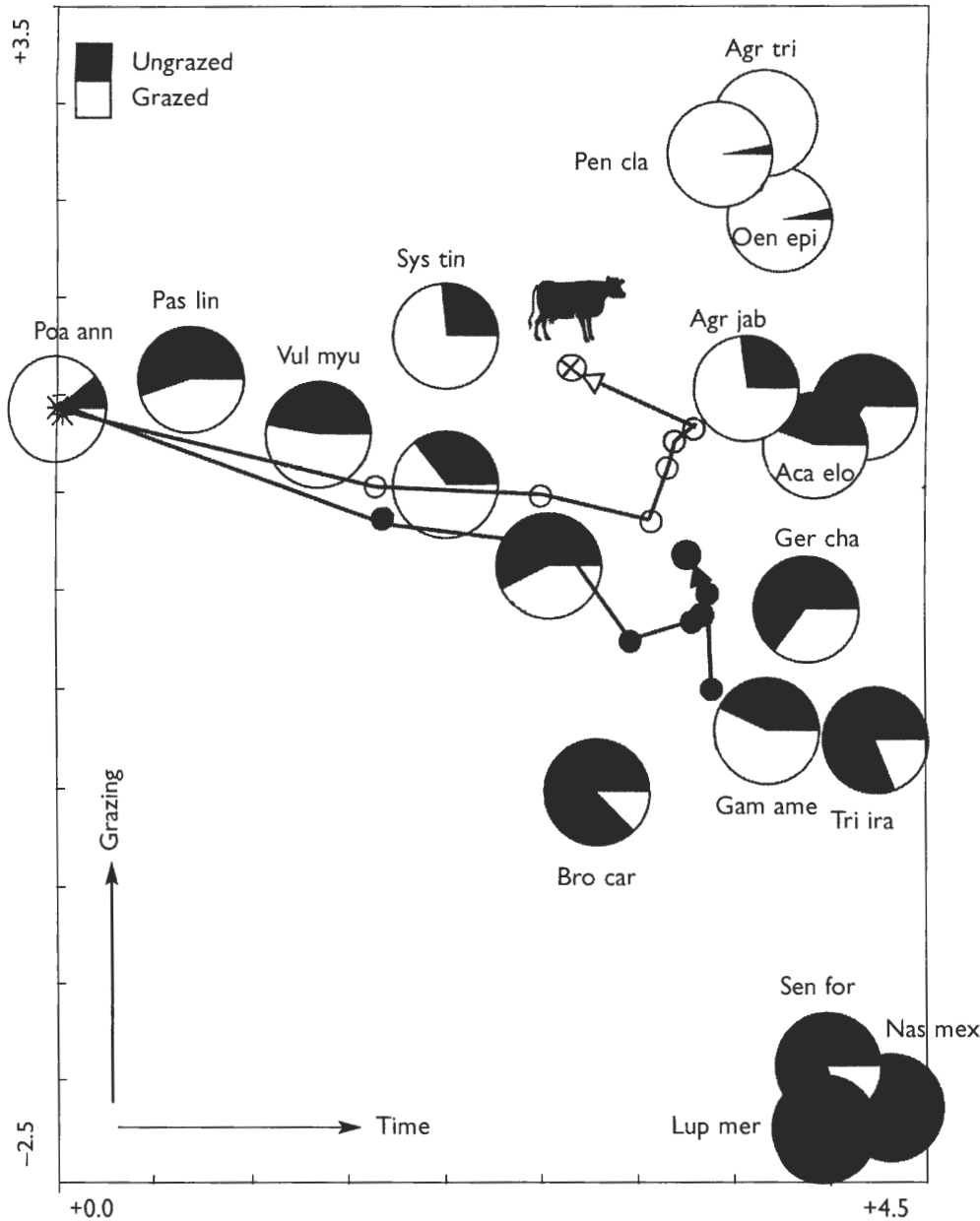
Figure 8.2
Successional trajectories in the first two axes of Detrended Correspondence Analysis of species abundance in the ungrazed (solid symbols) and grazed (hollow symbols) treatments of one of the young plots (0 years at the beginning)

The effect of grazing on vegetation structure was analysed during four years (twice a year). Circles indicate the relative abundance of each species in both treatments.

The following species are abbreviated using the first three letters of genus and species: *Poa annua, Paspalum lineisphata, Sisyrinchium tinctorum, Vulpia myurus, Lachemilla moritziana, Rumex acetosella, Penisetum clandestinum, Oenothera epilobifolia, Agrostis trichodes, Agrostis jahnii, Acaena elongata, Geranium chamaense, Trisetum irazuense, Gamochaeta americana, Bromus carinatum, Senecio formosus, Lupinus meridanus, Nassella mexicana.*

Source: Sarmiento, unpublished data.

MONITORING CHANGES IN SOIL PROPERTIES

The soils of the study area are characteristic of the Venezuelan paramo. They are inceptisols, with a sandy-loam texture, a high content of organic carbon and a very high proportion of stones. Changes in soil properties are particularly difficult to monitor in this kind of environment. Among the most important reasons for this are:

Figure 8.3
Detrended Correspondence Analysis of species abundance in the eight plots (young and old) and the two treatments (grazed and excluded) over four years (two samplings per year)

The first axis is correlated with time. Grazing is not correlated with any of the first four axis. No differences between grazed and excluded treatments were detected and for this reason we used the same symbol for both of them.

Source: Sarmiento, unpublished data.
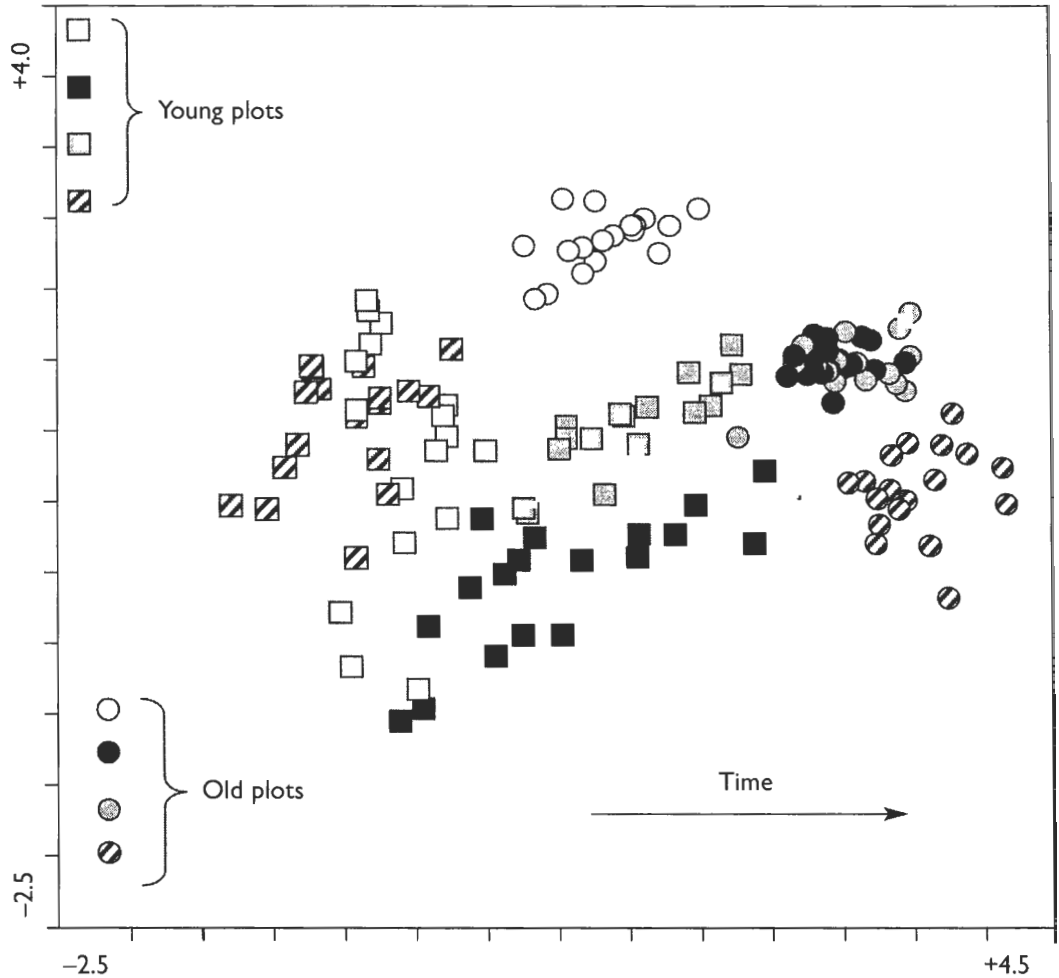
- the lack of response of many variables within a successional timescale
- methodological difficulties in detecting small changes in large ecosystem compartments (e.g. total soil organic matter carbon)
- high spatial heterogeneity in soil characteristics between study plots.

A synchronic analysis of some soil properties was performed in the same plots used for monitoring vegetation changes (Table 8.1). Internal variability within each successional category (between replicates) was very high for most variables. No significant temporal trends were detected for most of them.

An additional criterion to the analysis of variance, which makes it easier to visually evaluate which soil properties can be considered suitable indicators of change driven by those processes under study, is that the coefficient of variation should be lower between replicates (attributable to spatial heterogeneity) than within treatments or categories (attributable to the effect of the driving

Variable	Early succession (1–3 years) n=12	Intermediate succession (4–6 years) n=12	Late succession (7–9 years) n=12	Virgin paramo n=4	Mean of the groups n=4
Total C (%)	8.80 (31)a	9.40 (31)a	8.40 (36)a	11.20 (32)a	9.40 (13)
Total N (%)	0.42 (23)a	0.50 (21)ab	0.44 (28)a	0.61 (30)b	0.50 (17)
Microbial biomass (mgN kg⁻¹)	75.00 (24)a	76.00 (18)a	73.00 (16)a	177 (48)b	100.00 (51)
Microbial biomass (% of total N)	1.80 (30)a	1.60 (27)a	1.80 (41)a	2.90 (18)b	2.1.00 (30)
C/N	20.40 (10)a	18.70 (10)a	18.80 (15)a	18.40 (10)a	19.00 (4.8)
NH₄ (mg kg⁻¹)	0.90 (88)a	1.90 (60)a	2.00 (109)a	1.40 (76)a	1.60 (33)
NO₃ (mg kg⁻¹)	1.60 (85)a	1.40 (69)a	1.50 (115)a	1.70 (181)a	1.50 (7)
%NO₃	60.30 (49)a	45.30 (60)a	38.30 (88)a	22.70 (153)a	41.60 (38)
pH (H₂O)	4.80 (7)a	4.70 (5)a	4.90 (6)ab	5.20 (3)b	4.90 (4)
P (mg kg⁻¹)	18.40 (66)a	24.40 (84)a	32.20 (90)a	4.60 (48)a	20.00 (59)
CEC (meq 100 g⁻¹)	20.30 (29)a	23.20 (25)a	23.20 (25)a	23.90 (22)a	23.00 (7)
Ca⁺ (meq 100 g⁻¹)	3.10 (34)a	3.70 (33)a	3.70 (44)a	7.60 (90)b	4.5.00 (46)
Mg⁺ (meq 100 g⁻¹)	0.40 (48)a	0.30 (70)a	0.50 (80)a	1.20 (91)b	0.60 (68)
Na⁺ (meq 100 g⁻¹)	0.11 (14)a	0.09 (26)a	0.11 (18)a	0.120 (12)a	0.10 (12)
K⁺ (meq 100 g⁻¹)	0.35 (30)a	0.28 (33)a	0.32 (56)a	0.38 (39)a	0.30 (13)
Base saturation (%)	20.00 (31)a	19.90 (37)a	22.1 (65)a	38.20 (71)a	25.00 (35)

Table 8.1

Results of the synchronic analysis of soil properties along a secondary succession in Paramo de Gavidia

Note: Thirty-six plots with different fallow times and four virgin paramos were sampled. Different letters indicate significant differences between successional categories (ANOVA, a=0.05). Values in parenthesis are the coefficient of variation (%).

Source: modified from Llambí and Sarmiento (1998).

variables). It is obvious from Table 8.1 that the coefficient of variation between different successional categories was higher than within categories only for microbial biomass. Other variables, such as total C, C/N, mineral nitrogen and K⁺ presented a coefficient of variation between categories that was lower than within categories; thus they are not suitable as indicators of successional status. pH and to a lesser extent Ca⁺² and Mg⁺ presented similar coefficients of variation within and between groups, and hence, could be considered more suitable successional indicators. However, none of the analysed variables were sensitive at the timescale used to analyse succession (nine years) and only microbial biomass, pH, Ca⁺² and Mg⁺ were significantly lower in the successional plots than in the never-cultivated paramo. This last set of variables could consequently be considered appropriate as agricultural disturbance indicators. Due to the high intrinsic heterogeneity of these systems, it is not possible to conclude, based solely on this information, whether there are successional changes in these soil variables. The only possible conclusion is that heterogeneity is more important in explaining differences between plots than successional time.

In another study carried out in the same area, Abadín et al. (2002) used a stratified sampling technique to reduce spatial heterogeneity. They selected twenty-eight plots, in four different sectors of the valley and analysed thirty-two soil characteristics (but not microbial biomass). In each sector a complete successional sequence was sampled, trying to select plots on the basis of similar topographic, parent material and exposition conditions. The data for each sector were standardized before statistical comparisons were made. Abadín et al. found lower pH in cultivated plots and at the beginning of the succession, confirming the sensitivity of this variable. Apart from pH, the only other soil characteristic that was useful for monitoring successional changes was the $\delta^{15}N$ of soil organic matter, which decreases steadily along the crop–fallow–virgin paramo chronosequence. The behaviour of this

variable suggests that a change from 'open' to 'closed' N cycling is the characteristic that better discriminates these soils along succession.

Given the difficulty of detecting successional changes using synchronic methods, a diachronic analysis was carried out: the same plots presented in Table 8.1 were sampled again three years later. However, the differences between the two sampling dates (deltas) were not significant (paired t test) for any of the variables except Na$^+$ (Table 8.2). In the virgin paramo, where no temporal changes were expected, we observed a significant decrease in pH. The coefficients of variation of the delta values are very high for all variables, indicating that each plot responds in an idiosyncratic way (increasing, decreasing or maintaining the initial value). In conclusion, these variables were not sensitive in a three-year interval. Factor sensitivity could have been affected by spatial heterogeneity within plots (the ten points sampled to prepare a composite sample by plot may have been too few to provide a representative estimate) and inter-annual variability in other factors independent of successional driving processes (e.g. differences in climate or in grazing intensity between the two sampling years).

Table 8.2

Results of the diachronic analysis of soil properties along a secondary succession in the Paramo de Gavidia

Note: The same plots were sampled twice (in 1996 and in 1999). The values are the mean difference between both samplings (1999–1996). The per cent coefficient of variation is indicated in brackets. The cropped plots correspond to all plots that were in fallow in 1996 but cultivated afterwards. The other categories represent the seral stage at the beginning of the sampling interval. Asterisks indicate significant differences between the two sampling dates (paired t test, a=0.05).

Source: Abreu (2004)

Variable	Cropped n=16	Early succession n=8	Intermediate succession n=6	Late succession n=6	Virgin paramo n=4
Total C (%)	0.64 (295)	1.11 (241)	1.22 (108)	2.58 (184)	0.68 (157)
Total N (%)	−0.01 (900)	0.07 (114)	0.02 (150)	0.06 (300)	−0.05 (220)
Microbial biomass (mgN kg^{-1})	1.8 (1168)	6.9 (448)	0.7 (2237)	3.3 (860)	−18.6 (168)
C/N	−0.19 (3337)	−0.05 (13720)	1.59 (185)	5.99 (229)	3.39 (84)
pH (H$_2$O)	−0.45 (53)	−0.17 (159)	−0.12 (158)	−0.17 (159)	−0.25 (24)*
CIC (meq 100 g^{-1})	0.20 (3125)	−0.17 (2529)	−1.63 (177)	−2.84 (213)	−0.20 (4429)
Ca$^+$ (meq 100 g^{-1})	−0.18 (1022)	0.79 (228)	0.86 (178)	−0.11 (2836)	−1.95 (320)
Mg$^+$ (meq 100 g^{-1})	0.01 (2100)	0.11 (263)	0.14 (143)	0.03 (887)	0.50 (246)
Na$^+$ (meq 100 g^{-1})	−0.10 (30)*	−0.11 (9)	−0.10 (20)	−0.10 (10)*	−0.12 (17)*
K$^+$ (meq 100 g^{-1})	0.76 (99)	0.65 (142)	0.29 (86)	0.85 (92)	1.05 (170)
Base saturation (%)	0.80 (1193)	7.15 (154)	8.42 (150)	10.49 (223)	−0.05 (47000)

Monitoring in Heterogeneous Environments: Limitations and Challenges

Some possible generalizations about the limitations of monitoring in mountain heterogeneous environments are proposed in Figure 8.4. One of the main problems is spatial heterogeneity, which particularly limits the application of synchronic approaches. Figure 8.4A illustrates a case in which different individual plots present clear successional trends for the study variable, but when they are selected for a synchronic reconstruction of the succession (hollow circles in Figure 8.4A) the resulting dynamics does not represent underlying tendencies. Hence, when the effect of spatial heterogeneity is higher than the variable's temporal response, synchronic methods should not be used, at least not without the selection of more homogeneous plots using some valid criteria.

The second case, considered in Figure 8.4B, is the effect of plot history. In this specific example we suppose that part of the heterogeneity found in the study area is the result of different land
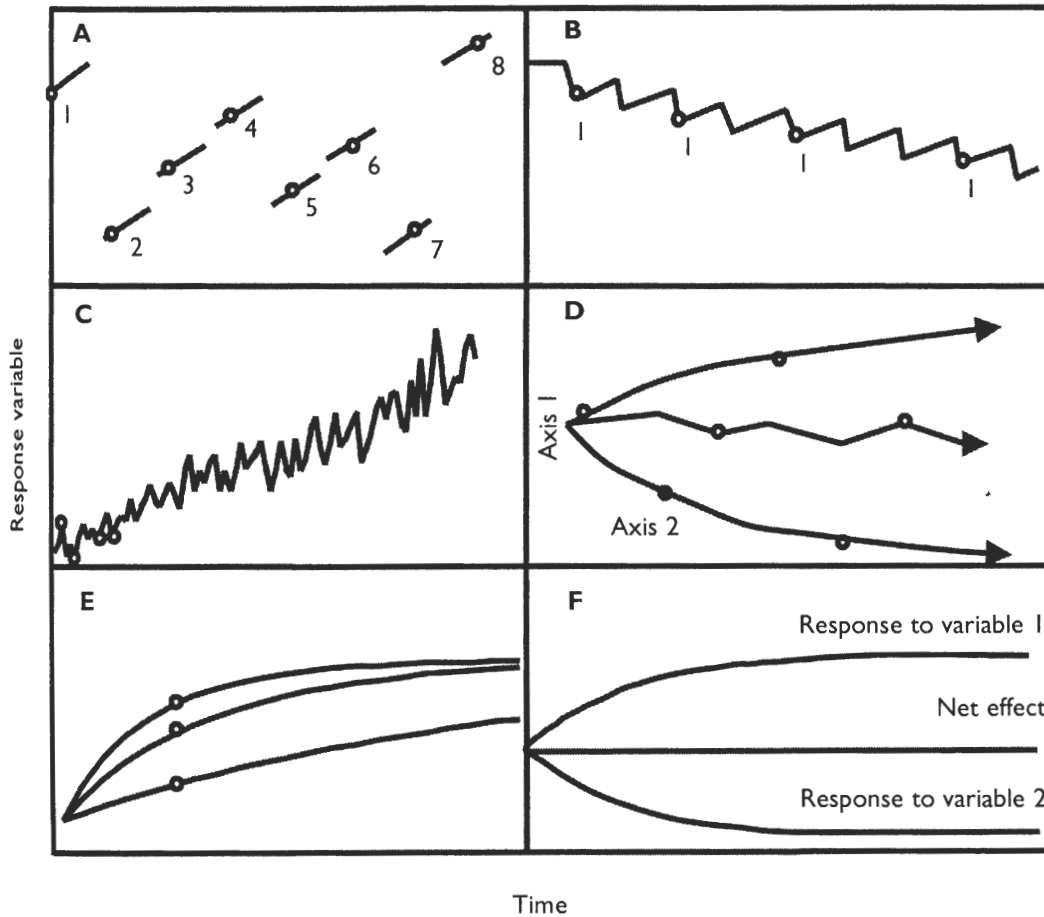
Figure 8.4
Different factors that can affect the results of monitoring succession in heterogeneous mountain environments

A. Spatial heterogeneity.
B. Different histories of land use.
C. High temporal variability (low stability).
D. Presence of divergent succes-sional pathways.
E. Different response rates.
F. Different state variables with opposite effects on the studied response variable.

use histories of the plots. In this region of the Venezuelan paramos, fallow agriculture has been prac-tised for less than a century. During this period, there has been a progressive incorporation of virgin paramo areas to the fallow system (Smith, 1995). If there is a progressive decline in the studied vari-able in successive cultivation–fallow cycles, and the plots selected for a synchronic analysis have experienced a different number of these cycles (like the one-year fallow plots in Figure 8.4B) the utilization of these plots as replicates would not be valid.

A third potential limitation is the inter-annual variability of the selected variable (instability), confounding diachronic analyses (Figure 8.4C). In this example, we assume that our hypotheti-cal variable is subjected to a high inter-annual variability and, as a consequence, successive sam-plings (represented by hollow circles in Figure 8.4C) are unable to detect the general trend in short-term studies.

Figure 8.4D illustrates the effect of successional divergence. In this example there are three possible trajectories, represented in a hypothetical ordination diagram of the vegetation. If plots with different successional times are selected (hollow circles) without considering the existence of divergence, the reconstructed trajectory would not correspond to any real successional pathway.

Alternatively, if all the selected plots are following the same pathway, only one of the three possibilities would be assumed as the general pattern.

Plots that change in the same direction but at different rates also introduce noise in the monitoring process (Figure 8.4E). Finally, Figure 8.4F illustrates the case in which two state variables acting in opposite ways on the response variable can reduce, modify or completely cancel out any measurable response (the problem of multiple causality).

Another important consideration for the success of monitoring is the selection of sensitive indicators. An ideal indicator responds significantly only to changes in one driving variable (temperature, grazing intensity, CO_2 in the atmosphere, land-use change, succession, rain, etc.). However, indicators are generally sensitive to several driving variables. In addition, indicators that are reported to be sensitive under some conditions may be less sensitive in other circumstances. For example, several authors reported microbial biomass to be an early indicator of changes in soil organic matter dynamics (Powlson et al., 1987; Carter, 2002), but in the case of paramo it was found not to be sensitive to marked changes in vegetation structure during the first twelve years of succession. The most sensitive indicator of soil changes analysed so far in paramo succession is the $\delta^{15}N$ of soil organic matter. $\delta^{15}N$ is an integrative ecosystem variable that indicates the nature of nitrogen cycling in the ecosystem. It would be interesting to explore the sensitivity of this variable for monitoring other processes than secondary succession after agriculture disturbance, such as land use or global change.

The study of secondary succession in the Venezuelan paramos illustrates the limitations of monitoring in spatially and temporally heterogeneous environments. These limitations relate mainly to the application of synchronic approaches. However, short-term diachronic approaches can also be hampered by temporal heterogeneity. The results presented here also suggest that succession in this kind of environment is characterized by divergent pathways and variable regeneration rates, and cannot be studied without taking into account this spatio-temporal complexity.

Which of the above limitations for monitoring secondary succession might apply to monitoring global change in mountain biosphere reserves? Given that mountains can generally be considered as heterogeneous environments, most of these limitations are potentially important in all mountain regions. In designing and interpreting monitoring systems, it is important to consider the likelihood of divergent pathways and the spatial variability of response times. Stratified samplings, large replicate numbers and the keeping of records of environmental variables in all plots can help to identify and interpret alternative pathways. Special attention needs to be paid to the generalization to large areas of results obtained in a particular set of conditions.

Finally, it is important to keep in mind that monitoring is only a descriptive (and static) procedure. To understand, interpret and predict ecosystem dynamics requires the analysis of the ecological processes and mechanisms that drive these changes, and involves the use of carefully controlled experiments and predictive simulation models. The formulation, calibration and validation of models, based on a solid knowledge of the structure and functioning of mountain ecosystem, is probably the best alternative to analyse the effects of global change, simulate different scenarios and explore mitigation measures. Carefully designed monitoring programs should provide the basic information for the validation of these ecological models.

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