

Arrested succession in pastures hinders regeneration of Tropandean forests and shreds mountain landscapes

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Summary

Arrested succession is conspicuous in the abandoned pastures of the Andean piedmont that have encroached upon the tropical montane forests toward higher limits and steeper slopes. Habitat 'shredding' is analysed to depict the current spatial configuration of tropical Andean landscapes, based on fragmentation patterns prompted by seed dispersal ecology and pasture encroachment.

Seed dispersal was studied to address the hypothesis that seed input constrains the recruitment of montane forest seedlings, thus impeding pasture conversion to forest. It turns out that a better competitor, the tussock grass *Setaria sphacelata*, is limiting dispersal success due to its bioarchitecture and planting patterns. Because of the variegation of fragments, the area is in danger of landscape homogeneity within a matrix of degraded pasture. Currently, protection of fragmented remnants and restoration of original landscape structure and function are urgent needs for land-use planning toward sustainable development in the region.

Restoration ecology is plausible as a means of conservation for degraded Tropandean forests, since human impacts have shredded landscapes entirely. Dispersal ecology may be used to facilitate pasture conversion to forest in equatorial landscapes, but the proactive approach of pasture removal or planting strategy should differ from that for lowland Amazonia, where abandoned pastures are different from those of montane environs. However, the region may be proactively managed only if political decisions include conservation as a goal of development.

Keywords: seed dispersal, habitat fragmentation, forest conversion, landscape restoration, tropical Andes, Ecuador

Introduction

There is a dearth of information on the ecology of tropical mountains. Recent specialized conferences pointed to the necessity of further conservation work in the cloud forest belt

(Hamilton *et al.* 1993), as well as in the entire neotropical montane forest zone (Churchill *et al.* 1995). In Ecuador, the tropical Andes region (Tropandean for short) represents approximately 40% of the area of the country. The topographic complexity of the Tropandean ecoregion produces a number of bioclimatic zones, which make Ecuador one of the most biologically-diverse nations per unit area (Pearman 1995) in the neotropics. The Andean *piedmont* is the ecotonal belt of montane foothills where lowland forests and highland grasslands (or *páramos*) overlap. Hence, the piedmont shelters much of the biodiversity which is endangered by the current land use of montane landscapes (Wethrich 1993). However, human pressure is so great that the zone has been considered 'anthrophilous' in one geobotanical classification (Acosta-Solis 1977).

Human impacts have been a decisive force in shaping the landscape configuration of tropical mountains in general (Budosky 1968). Ellenberg (1979) pointed out that the extent of human influence on tropical mountain ecosystems in South America has not been fully assessed, although in Ecuador, and most of the Andean region, the imprint of human impact is easily determined, even in areas with established forests (Denevan 1992; Sarmiento 1994). Recently, the attention given to the conservation of cultural landscapes has shifted from the traditional approach of preservation of 'pristine' primary tropical rain forests towards the restoration and proactive management of Tropandean landscapes (Naveh 1994; Denniston 1995; Sarmiento 1995a).

Pasture conversion and habitat fragmentation

Pasture is now a pervasive attribute of Andean landscapes. Savannization started when people synchronized lowland-highland transhumance of herds and fuelwood gathering to a stable pattern 8000 years ago (Quintanilla 1983) and when present-day forests appeared in their mosaic pattern (Gentry 1982). Nevertheless, it is still difficult to define the actual configuration of previous landscapes, since ancient changes were wrought by fires. Burning was the driving force for establishment of the anthropogenic grasslands in the páramos. Læggaard (1992) stated that the grassland páramos is the result of anthropogenic burning; fire has many times reshaped the original highland Andean forests, where tussock grasses have taken over, along with associated pyrophytic shrubs (Lauer 1979). More recently, the encroachment of pasture as the

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dominant feature of tropical landscapes of the Andean piedmont, has been prompted by livestock development programmes, as discussed by several authors (Bushbacher 1986; Rudel & Horowitz 1993; Aide & Cavellier 1994; Lugo & Lowe 1995).

Seed dispersal for pasture conversion

The forest matrix, which has been ecologically reshaped many times by earthquakes, volcanic eruptions, flood and fire, is also drastically affected by clearcutting (Millones 1982). Clearcutting for agriculture opened frontiers in mesic environments of mild weather patterns, where African grasses (locally known as *kikuyo*, mainly *Panicum clandestinum*) were introduced for cattle ranching, and constrained dispersal success. At lower elevations, imported grasses (i.e., the genera *Brachiaria*, *Setaria* and others) have also been intrusive in the piedmont. Some natural pastures (i.e., *chirimilla*, *Digitaria sanguinalis*) can revert to forest in a direct successional sequence after abandonment, which is the

basis for some conservation recommendations in the lowland tropics (Cardoso da Silva *et al.* 1996); however, this is a difficult option in the Tropandean ecoregion where arrested succession of *pasto miel* (*Setaria sphacelata*) pastures is shaping different patterns of habitat fragmentation, with forest remnants kept only towards the upper reaches of steep slopes and ridges (Myster & Sarmiento 1997). With this rather linear pattern, which contrasts with the checker-board array in temperate forests, Feisinger (1994) argued that in the tropical Andes, fragmentation should be considered rather as 'habitat shredding', which expands on Janzen's (1987) original observation of what he called 'habitat sharpening' in the tropics. Here I argue that shredding is maintained by arrested succession in abandoned pastures where recalcitrant seeds are not able to start succession back to forest.

To a large extent, Tropandean landscapes have been fragmented in five ways (*sensu* Harris & Silva-López 1992): (1) *regressive fragmentation, R*, occurs up the hills from the valleys' bottomlands, pushing back the forest edge to successively higher limits and on steeper slopes, filled with

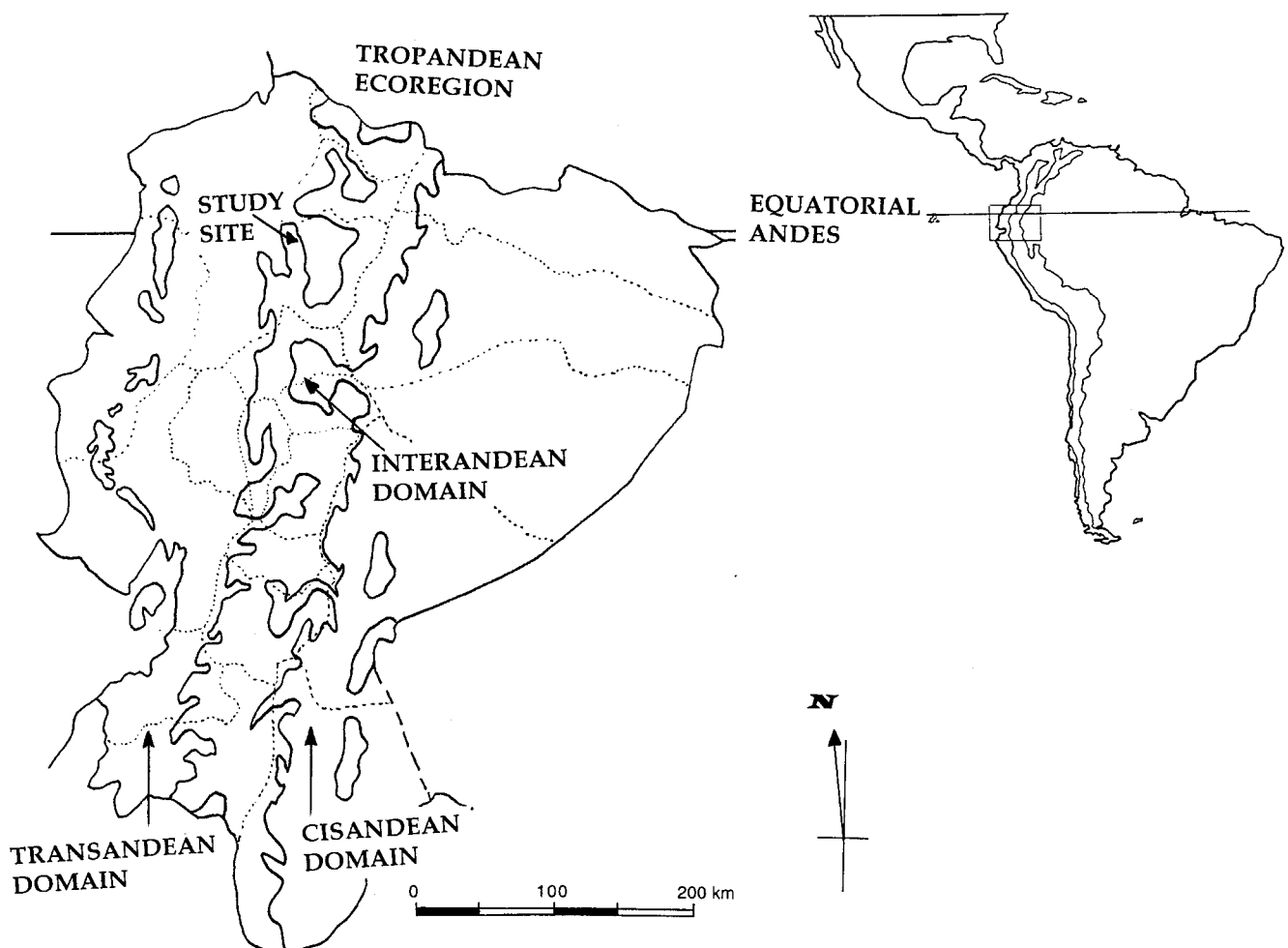


Figure 1 A schematic arrangement of the three domains of Tropandean landscapes in Ecuador and location of the study site. The eastern slopes of the Andes (Cisandean), the highland plateau (Interandean) and the western flanks (transandean) constitute more than 40% of the country.

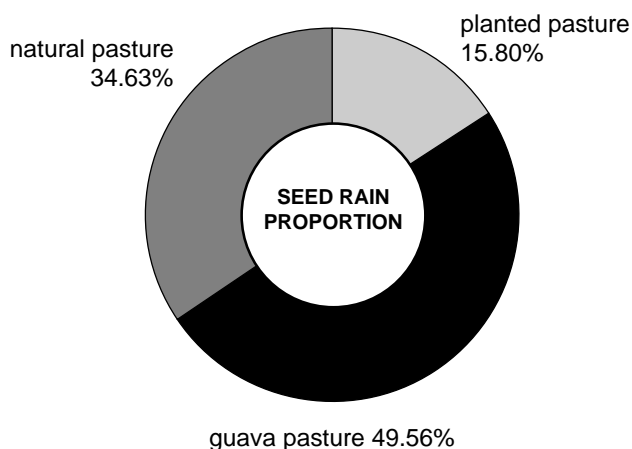


Figure 2 Differential seed rain in the three pasture types. Planted pasture with *Setaria sphacelata* receives comparatively less seed fall than the natural pasture and the guava pasture.

pies-de-vache, which are erosive ravines due to trampling; (2) *enveloping fragmentation*, *E*, occurs around semi-circular forest patches, which are left within the agricultural landscape as shade for cattle or on top of hilly terrain where grazing is inaccessible; (3) *divisive fragmentation*, *D*, occurs along the road sides, which allow strip development in towns created by the transient goods and services for trade; (4) *intrusive fragmentation*, *I*, by clearings within the few high Andean protected areas, which create dynamic amorphous boundaries crossed to reach open-access grazing grounds or montane forest patches that are infilling a gap or clearing in fragile slopes; and (5) *encroaching fragmentation*, *C*, which compromises the survival of linear relicts along river banks and brooks, where ranchers prevent herding, thus generating riparian corridors in galleries of dissected terrain. A shredded landscape is typical of the montane forests of tropical America. In time, this spatial configuration follows the trend of the landscape's anthropogenic modification (Sarmiento 1982), which exhibits a cascading effect from forest to pasture, to agricultural fields,

to cities, to deserts. This effect has sharpened the variegated landscape mosaic to the present day pre-desertic slope lands.

The principal aim of my study was to determine if the ecological processes of seed dispersal and forest regeneration are imperiled by the fragmentation pattern in the mountains, in a way which might explain the limited or absent regeneration of the forest community once pasture has been established. If seed dispersal is the clue, the management of forest fragments to enhance bird- or bat-dispersed plant species might help in the restoration effort. As different grass species are used in pastures, it was important to determine which pasture type can not revert to forest by succession, and why.

Methods

The chosen area with secured abandonment included three different pasture types. Standard seed dispersal methods and techniques were used to assess the seed input, the seedling germination, the sapling establishment and the recruitment of the regenerating community in the area.

Study site

The site for the study of seed dynamics and forest regeneration in abandoned pasture was the Maquipucuna Reserve (0°05'N 78°37'W), and adjacent sites in north-western Ecuador (Fig. 1). This is a private reserve on the Nanegal Range of the upper Guayllabamba River basin. Altitudinal transect studies (Raguso & Gloster 1993; Sarmiento 1994) show that the habitat affinities in taxa often respond to impacted systems, with secondary old-growth, bamboo thickets, successional meadows, young secondary forest regrowth, forest edges and riparian forests with abandoned pastures and old fields located towards the flattened lower portion (c. 1400 m elevation) of the reserve. Ash and tephra originated from two nearby volcanoes with Plinian eruptions, which blanketed evidence of ancient human occupation of the land. The

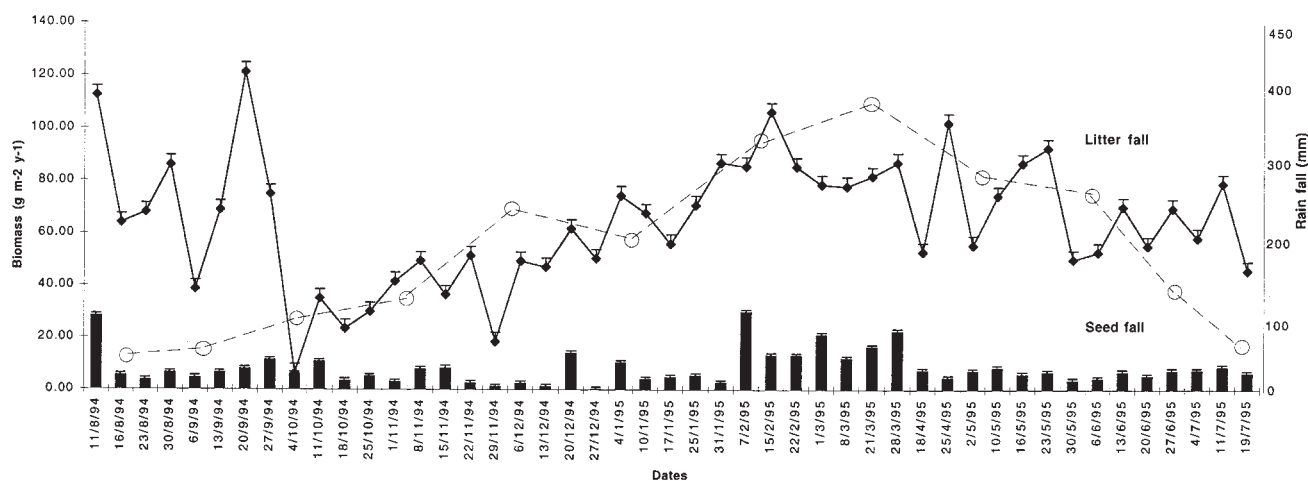


Figure 3 Variation in litter fall (including leaves, twigs, etc.) with seedfall in weekly samples and seasonality of rainfall regime. Error bars are + 1 SE.

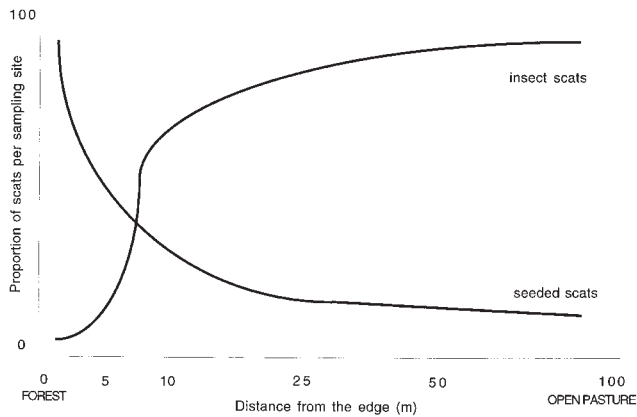


Figure 4 The relationship between distance from the forest edge and type of scats present, indicating ornithocory toward the edge, promoting a 'border effect' in the boundary. Insectivory prevailing in the open pasture did not contribute to seed dispersal, thus aiding pasture encroachment.

rainfall regime shows a typical tropical pattern, a dry season from mid-June to late-September with a minimum in July, and a rainy season from October to late May with a maximum in March. The daily temperature varies between 14°C and 27°C, but this change is constant throughout the year, regardless of the season. A full description of the area is presented elsewhere (Sarmiento 1995b).

Techniques

For three years (1993–95), I followed the dynamics of seed dispersal for pasture conversion through studies of seed rain, seed shadow, seed removal (predation) and seed germination, in three pasture types occurring adjacent to old-growth forest. A Geographical Information System (GIS) model of fragmentation in the area was performed with an Arc/INFO 6.1 Triangular Irregular Network routine (TIN; ESRI 1995), supported by Ground Positioning System (GPS) Magellan 3.2 data and ground truthing. Natural *chirimilla* (*Digitaria sanguinalis*), planted *pasto miel* (*Setaria sphacelata*) and *guayaba* (*Psidium guajaba*) pastures were subjected to location analysis and randomly assigned blocks for the treatments of seed rain, seed shadow, seed removal and seed germination. A modified Gorchov's (1993) design of 30 1-m² seed traps and 32 0.25-m² regenerating exclosures were systematically checked for seed records and seedling occurrence on a weekly basis. Circular plots of 10 m² diameter were used to study vegetation dynamics. Plant inventories used additive importance values ($IV = \sum rDn + rFr + rDo$), through summation of relative density ($rDn = \text{number of individuals of species A} \times [\text{total individuals of all species in sample}]^{-1} \times 100$), relative frequency ($rFr = \text{number of plots with species A} \times [\text{total number of plots for all species}]^{-1} \times 100$) and relative dominance ($rDo = \text{basal area of species A} \times [\text{total basal area for all species}]^{-1} \times 100$) to establish plant oligarchies in the

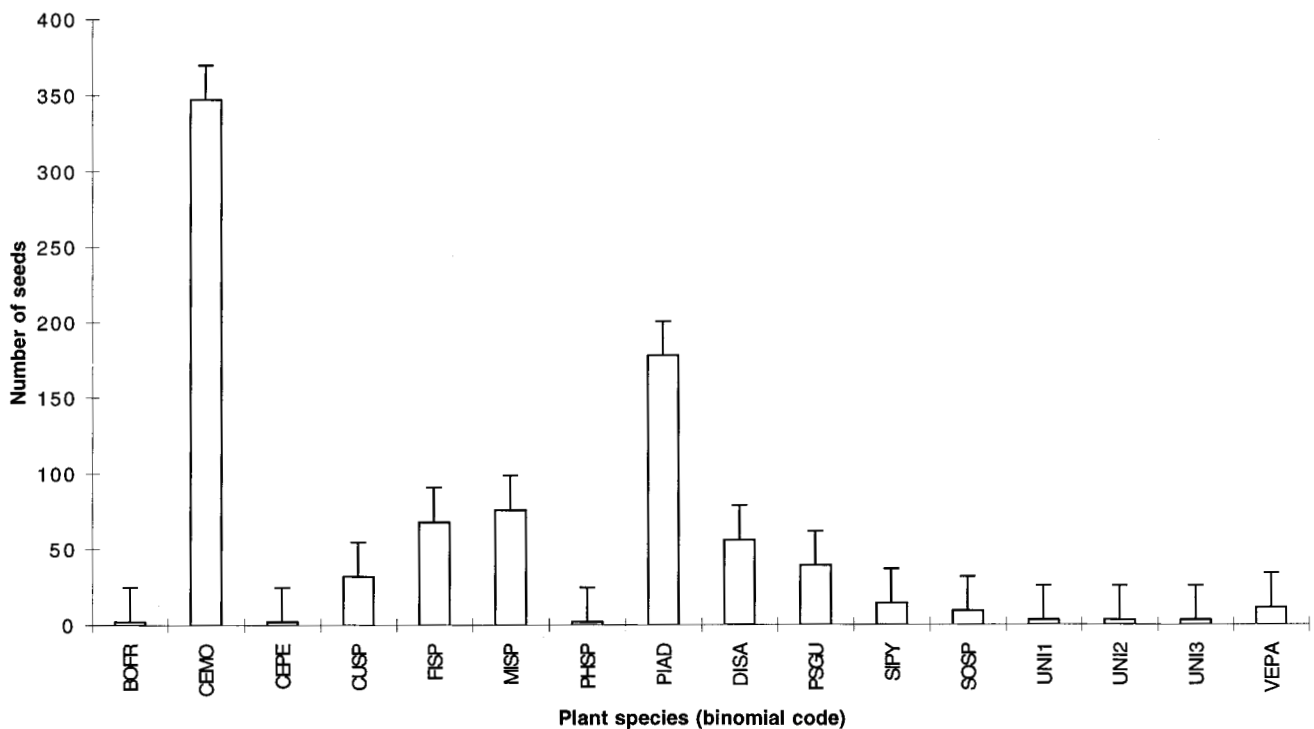


Figure 5 Preferred food sources of collected and bagged birds and bats; shows the contribution of the seed shadow for potential regeneration. BOFR: *Bocconia frutescens*; CEMO: *Cecropia monostachya*; CEPE: *Ceiba pentandra*; CUSP: *Cuphea* sp. (cf. *cartagenensis*); FISP: *Ficus* sp. (cf. *insipida*); MISP: *Miconia* sp. (cf. *aeruginosa*); PHSP: *Phyllanthus* sp. (cf. *niruri*); PIAD: *Piper aduncum*; DISA: *Digitaria sanguinalis*; PSGU: *Psidium guajaba*; SIPY: *Siparuna pyrygena*; SOSP: *Solanum* sp. (cf. *acerifolium*); UNI1: Unidentified 1; UNI2: Unidentified 2; UNI3: Unidentified 3; and VEPA: *Vernonia patens*. Error bars are +SE.

Table 1 A list of plants from the regenerating community growing as seedlings underneath *Setaria sphacelata* pasture after one year of exclusion. Abundance of Asteraceae and other forbs is expected after abandonment of old fields, but is also present here after pasture abandonment. However, they do not recruit as saplings between the tussock grasses. Note the lack of seedlings from tree species in all sample sites (B1 through B7) of regenerating exclosures.

<i>Plant</i>	<i>Sample Sites</i>							<i>% of total</i>
	<i>B1</i>	<i>B2</i>	<i>B3</i>	<i>B4</i>	<i>B5</i>	<i>B6</i>	<i>B7</i>	
<i>Ageratina pichinchensis</i>	0	0	0	3	0	0	0	0.16
<i>Ageratum</i> sp.	0	0	0	0	3	0	0	0.16
<i>Anagallis minima</i>	0	0	0	6	0	0	0	0.33
<i>Asplenium</i> sp.	4	0	0	0	0	1	0	0.28
<i>Axonopus scoparius</i>	0	0	0	0	0	163	17	10.13
<i>Baccharis</i> cf. <i>latifolia</i>	0	0	0	7	0	0	0	0.39
<i>Begonia parviflora</i>	3	0	0	0	0	0	0	0.16
<i>Bidens pilosa</i>	0	0	0	0	0	1	1	0.11
<i>Bocconia frutescens</i>	0	0	0	0	0	2	0	0.11
<i>Bohemeria ramifolia</i>	0	0	0	0	1	6	0	0.39
<i>Borreria acymoides</i>	1	1	4	0	0	0	0	0.33
<i>Coniza floribunda</i>	0	0	1	0	0	0	0	0.05
<i>Cuphea cartagenensis</i>	3	0	0	14	4	6	2	1.63
<i>Cyathula chyranthoides</i>	0	0	0	0	0	0	3	0.16
<i>Cyperaceae 1</i>	3	0	0	0	6	0	0	0.51
<i>Cyperus</i> sp.	0	0	0	0	0	14	0	0.78
<i>Cyperus diffusus</i>	0	0	0	3	1	0	2	0.33
<i>Cyperus hermaphroditus</i>	15	0	0	74	0	3	1	5.23
<i>Desmodium canum</i>	0	0	0	0	0	8	0	0.45
<i>Desmodium intortum</i>	0	0	0	2	0	0	5	0.39
<i>Digitaria sanguinalis</i>	1	0	56	72	0	40	57	12.71
<i>Drymaria ovata</i>	0	0	0	0	0	4	0	0.22
<i>Elephantopus mollis</i>	0	0	0	0	2	0	0	0.11
<i>Galinsoga quadriradiata</i>	7	0	0	0	0	0	0	0.39
<i>Hydrocotyle leucocephale</i>	32	0	11	6	2	11	21	4.67
<i>Iresine diffusa</i>	8	0	2	3	0	1	4	1.01
<i>Justicia camata</i>	0	0	22	3	23	0	0	2.75
<i>Liquen</i>	0	9	0	0	0	0	0	0.51
<i>Mickania cordifolia</i>	0	1	0	0	0	3	1	0.28
<i>Miconia</i> cf. <i>aeruginosa</i>	9	0	0	7	2	2	1	1.18
<i>Mimosa albida</i>	0	0	0	0	0	1	0	0.05
<i>Oxyptalum cordifolium</i>	0	0	0	0	1	0	0	0.05
<i>Panicum</i> sp.	0	2	0	0	0	0	0	0.11
<i>Paspalum conjugatum</i>	0	0	48	0	0	0	0	2.7
<i>Penax hirtus</i>	0	0	2	0	7	5	30	2.47
<i>Phyllanthus niruri</i>	4	0	0	4	0	0	0	0.45
<i>Piper aduncum</i>	0	0	0	14	1	0	0	0.84
<i>Piper phytolaccaefolium</i>	4	1	0	6	0	0	0	0.61
<i>Pseudechinolaena polystachya</i>	0	0	0	0	24	0	0	1.35
<i>Pseudelephantopus spiralis</i>	21	19	71	83	25	6	19	13.73
<i>Psidium guajava</i>	0	2	1	0	0	0	0	0.17
<i>Pteridofita 1</i>	6	0	0	0	0	1	0	0.39
<i>Selaginella diffusa</i>	38	0	0	4	0	1	5	2.7
<i>Setaria parviflora</i>	0	0	7	0	0	0	0	0.39
<i>Setaria sphacelata</i>	120	333	0	0	0	0	0	25.59
<i>Sida rhombifolia</i>	0	2	0	3	0	0	0	0.28
<i>Solanum</i> sp.	0	0	0	0	0	1	0	0.05
<i>Solanum acerifolium</i>	0	0	0	2	0	1	2	0.28
<i>Solanum caripense</i>	2	0	0	0	0	0	0	0.11
<i>Sporobolus poiretii</i>	0	0	0	0	0	0	15	0.94
<i>Stachytarpheta cayannensis</i>	0	1	1	0	0	0	0	0.11
<i>Tripogandra serrulata</i>	0	0	0	0	0	0	3	0.16
<i>Verbena litoralis</i>	5	0	0	0	0	0	0	0.51
<i>Vernonia patens</i>	0	0	1	1	0	0	2	0.05
Total (<i>n</i> = 1777)	286	373	226	317	102	282	191	
Total % of seedlings	16.11	20.99	12.72	17.83	5.74	15.87	10.74	100%

Table 2 The seed removal results are expressed as a removal index on different locations: forest interior (FOREST), forest edge (FEDGE), *Psidium* pasture edge (GUAVA1), *Psidium* pasture interior (GUAVA2), *Setaria* pasture edge (PEDGE), *Setaria* pasture interior (PAST1) and *Digitaria* pasture interior (PAST2). Note the variation of results among small seeds and big seeds, some of which were never removed; also, note the contrasting trend of seed removal from the pasture sites during rainy and dry seasons.

Season	Seed Type	FOREST	FEDGE	GUAVA1	GUAVA2	PEDGE	PAST1	PAST2	Mean
Wet Season	Rice	1.00	1.00	0.73	0.86	0.73	1.00	1.00	0.91
	Peanuts	0.93	1.00	0.80	0.80	0.93	1.00	0.56	0.86
	Fig	0.41	0.23	0.40	0.20	0	0.60	0.26	0.30
	Tomatillo	0.23	0	0.06	0	0	0	0	0.04
	Guava	1.00	0.93	0.60	0.86	0.66	1.00	1.00	0.86
	Guaba	0	0.10	0	0.06	0.10	0.33	0.26	0.12
	Caimito	0	0	0	0	0	0	0	0
	Coroso Palm	0.16	0.06	0	0	0.23	0	0	0.06
	Carachacoco	0	0	0	0	0	0	0	0
	Mean	0.39	0.36	0.28	0.31	0.29	0.43	0.34	
Dry Season	Rice	1.00	1.00	1.00	1.00	0.73	1.00	1.00	0.96
	Peanuts	1.00	0.86	1.00	1.00	0.93	0.8	0.86	0.92
	Pagche	0.50	0.33	0.60	0.33	0.66	0.26	0.33	0.43
	Tomatillo	0.50	0.16	0	0.16	0	0.16	0	0.14
	Guava	1.00	1.00	1.00	0.86	1.00	0.93	1.00	0.97
	Chirimoya	1.00	0	0	0.50	1.00	0	0	0.35
	Caimito	0	0	0	0	0	0	0	0
	Carachacoco	0	0	0	0.66	0	0	0	0.09
	Mean	0.62	0.41	0.4	0.56	0.54	0.39	0.39	

pasture (Campbell 1994). Summation of the three parameters (total = 300) provided an unbiased estimator of the importance of a plant species in relation to the entire sampled community; thus, these oligarchies determined the few species that control the montane landscape pattern as a whole. I also placed artificial bamboo perches and collectors to encourage roosting of forest-dwelling birds. I captured seed shadow data by mist-netting frugivorous birds and bats, checked for phoresic seeds (ectozoochory) and bagged them to obtain seed samples from regurgitated and defaecated material (endozoochory). The C:N ratio of faecal material was analysed, separating guano from frass, insects and pellets, to check for enhancement of germination of seeded scats, applying pulverization of samples and C and N determination. Seed shadow was also recorded during random walks in the pasture, where distance to the forest edge, type of scat and seed content were recorded. Germination assays were carried out using soil samples for determination of the seed bank and the potential for germination of certain common species. Enhancement of the germination of guava trees by manure application was also investigated to establish the effect of pastoralism and regeneration using palatable seeds of guava as pioneer tree species for forest recovery. Force-fed guava seeds in horse manure were compared with a control experiment each germinated in twenty 5-cm-diameter plastic vials under shaded conditions for a month. Seed predation was analysed using 25 scattered feeding stations; they provided data for removal rates of eleven different types and sizes of seeds in the three different pastures with five separate overnight exposures. Removal index, obtained from the proportion of seeds originally placed and seeds remaining the

next day, shows the number of seeds taken as a function of the number of the seed pool in feeding episodes.

Results

Over the course of this study, a total of 24 011 seeds from at least 20 families and 57 plant species were recorded from seed traps. Seed rain varied between pasture types (Fig. 2). Planted pastures received less seed input than the other pasture types, and that either from endozoochory (13.2% of seeded scats) or anemochory (15.8% of seed fall). Seed density was almost 10% of the total litterfall, with seed rain of approximately 366.5 g m⁻²; in contrast, the annual biomass of leaves, twigs and others was 89.19% (3026.78 g m⁻²) of a total cumulative biomass of 339.33 kg ha⁻¹ y⁻¹. The range of the mean density of seed rain per seed trap varied from 39 to 4610 seeds m⁻² y⁻¹; the maximum number of seeds recorded from any one trap during any sampling collection was 760 seeds m⁻² 7d⁻¹ at the peak of the rainy season (21 March 1995). Significant differences in seed rain accumulation were found among planted, natural and guava pasture (two-way ANOVA, $F = 3.2$, $p < 0.05$). Guava was significantly different from the rest (two-way ANOVA, $F = 7.2$, $p < 0.05$) and in it, small N-fixers and mycorrhizal facultative *Psidium guajaba* trees provided perching stations and enhanced overall seed dispersal, with 46.57% of the pooled seed rain accounted for.

Seed fall and litter fall showed synchrony with rainfall episodes (Fig. 3), with higher values during the rainy season. The contribution from seeded scats on seed traps to the seed shadow was largely concentrated at the forest margin. No fae-

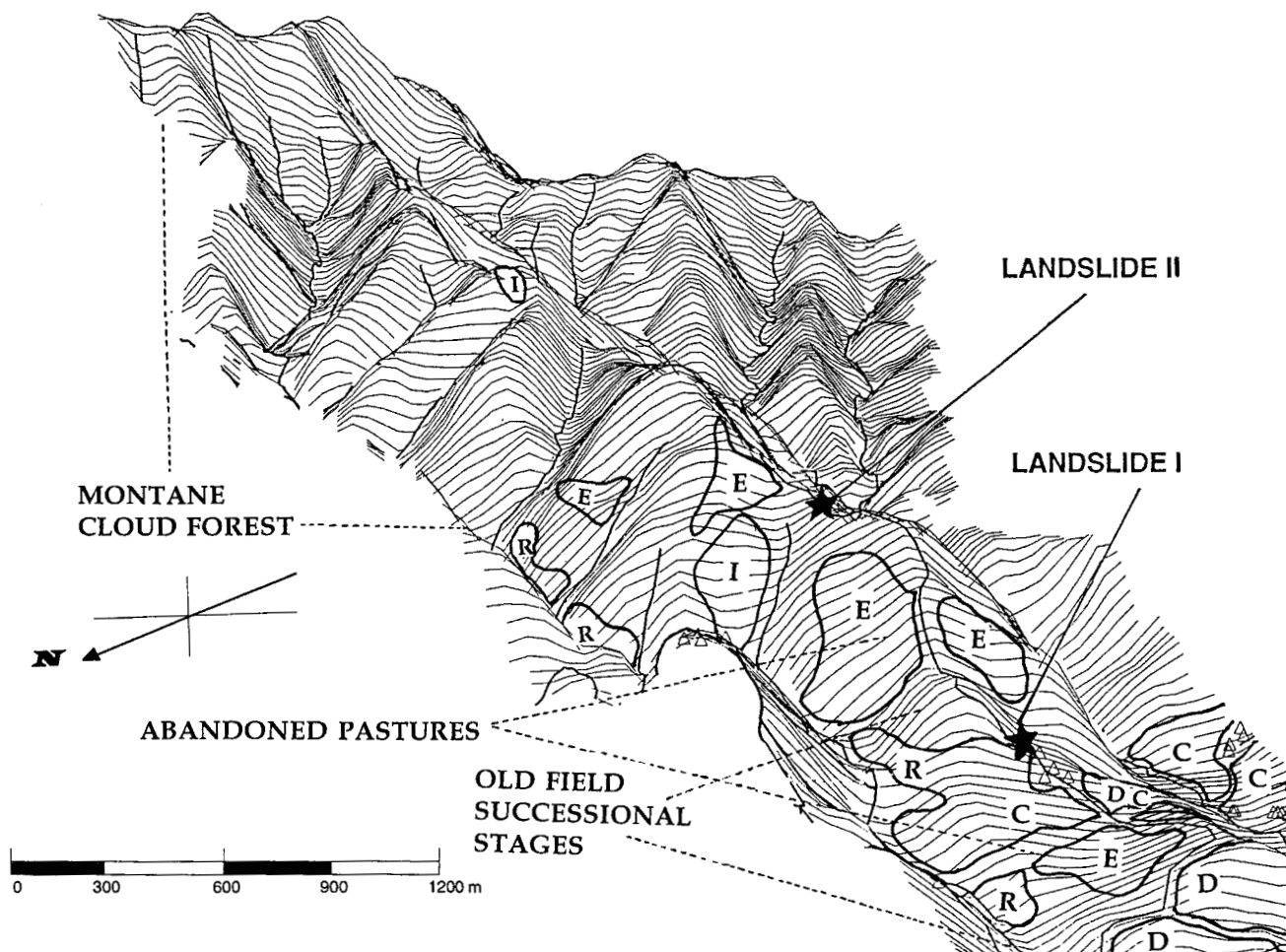


Figure 6 Digital elevation model (DEM-GIS) of the Maquipucuna Reserve, showing the array of different types of fragmentation operating in the area: R, regressive; E, enveloping; I, intrusive; D, divisive; and C, encroaching.

ces-containing seeds were collected up to 25 m from the forest margin, while scats with insect remains increased with distance from the forest edge into the pasture. There was a negative correlation between endozoochory and distance from forest edge (Spearman Rank Correlation, $R_s = -0.7$, $n = 465$ [total dropping count]), but a positive correlation between pasture core and non-seeded scats (Fig. 4). Preferred food sources for frugivorous animals were *Cecropia monostachya*, *Piper aduncum*, *Miconia aeruginosa* and *Ficus insipida* seeds, which were collected from either bird or bat scats, and made a large contribution to the seed shadow (Fig. 5).

The regenerating community is represented by seedlings from 58 species, including lichens, mosses, ferns and fungi underneath the canopy of tillers from *Setaria* (Table 1). There were no observations of seedlings of montane forest tree species within the pasture; unlike the *Psidium guajaba* saplings found in the pasture, the saplings of forest species present in the plots are sprouting from older root stock and stumps left after clearcutting of montane forest.

The regeneration assay showed no significant difference (one-way ANOVA, $F = 0.29$, $df = 26$, $p = 0.9$) in manure-

embedded seeds; washing of seeds, planted with or without manure, actually reduced biomass in comparison with controls. The seeded scat C:N ratio was 30.82 for insects, 37.29 for pellets, 4.28 for frass and 2.09 for guano. The highest values of total N in the samples came from guano scats (19.52%). Seed records seldom came from insect scats, which reflects the separation of frugivory in the forest edge versus insectivory in the open pasture.

There were differences in seed removal amongst sites and between dry and wet seasons (Table 2). Importance values of the vegetation plots clearly showed oligarchies in the pasture community, with dominance of *Axonopus scoparius* (IV = 182.41), *Piper aduncum* (IV = 117.16), *Digitaria sanguinalis* (IV = 293.72), *Psidium guajaba* (IV = 186.35), *Setaria sphacelata* (IV = 289.9), *Sida rhombifolia* (IV = 103.31) and *Vernonia patens* (IV = 98.56). These and other data were used to calibrate the potential vegetation in the fragmentation model of the reserve (Fig. 6), which portrays the likelihood of fragmentation patterns previously mentioned (either C, D, E, I, R, or a mixture of them) along the trail and the different land-use practices, including abandonment. The shredding

of the montane forest is evident along the trails and by the rivers and ravines, which explains the correlogram of forest remnants and slope steepness.

Discussion

Fallow and abandonment does not always trigger succession as expected (Myster & Pickett 1990, Goodwell 1992). In common with the results Harden (1996) obtained for erodibility in southern Ecuador, I found pasture encroachment leading to exacerbated degradation with abandonment, as well as constrained dispersal of recalcitrant seeds, in *Setaria sphacelata* pastures. This finding contrasts with the supposition that pasture plants provide 'safe sites' to enhance germination of tree species of the lower-altitude montane tropical forests, as in Sierra Nevada de Santa Marta, Colombia (Aide & Cavellier 1994). Sprouting of old stumps brings back forest species (i.e. shade-tolerant species) amidst the open pasture, but frugivory contributes to the dispersability of edge-tolerant species. After seeds of pioneer bird-dispersed shrubs (i.e., *colca*, *Miconia* cf. *aeruginosa*, Melastomataceae) have been recruited into the pasture from neighbouring forest patches, progressive succession may proceed (Whitmore 1983). Natural tropical pastures may follow modified successional pathways (Gibson & Brown 1992) with the added contribution of bat-dispersed plants (i.e., *cordoncillo*, *Piper aduncum*, Piperaceae). Curiously, by dispersing seeds while flying, the spatial flight pattern of birds (across the edge) and bats (along the edge) may determine the outcome of the regenerating community. However, unlike Amazon (Cardoso da Silva *et al.* 1996) or Costa Rican sites (Loiselle *et al.* 1996), pioneer tree species from endozoochorous seeds (i.e., *guarumo*, *Cecropia monostachya*, Cecropiaceae) do not form monospecific stands in the gaps and are rarely observed as saplings in tropical montane forests. My observation (Sarmiento 1997) is that they encroach on the forest edge even further, developing true ecotonal characteristics in the 5 m between the forest remnant and the open pasture. Also contrasting with a suggestion for restoring lower subtropical forest sites in Florida (McClanahan & Wolfe 1993) or in Colombian lowland tropical sites (Aide & Cavellier 1994), there was no statistical confidence ($\alpha = 0.05$) in the contribution of baited perches to seed shadow in the study site, a result which was also recorded by Holl (1995) for a montane site in Costa Rica. Manure embedding was conventionally considered as an evolutionary advantage of endozoochorous seeds (Alvarez-Buylla & García-Ramos 1991); however, my findings in montane tropical forests on volcanic soils (Sarmiento 1997) show that this trait is not as evident as expected for tree species recruitment in the lowland tropics.

Attempts at reforestation of degraded pastures have not yet proven to be an efficient landscape rehabilitator for the area. The use of *Inga*, *Alnus* or *Erythrina* as nitrogen-fixing trees is promoted for soil fertility considerations (Lieth & Lohman 1991); however, none of them shows potential to enhance zoochory, as does *Psidium guajaba*, the guava tree. I ob-

served that using this native tree might 'jump-start' succession back to forest if planted following the peninsular contouring of slope terrains. Of course, reforestation efforts are mostly concerned with sustaining wood yields for human consumption. For instance, eucalyptus trees (*Eucalyptus globulus*) were introduced as a panacea for tropical forestry. *Eucalyptus* plantations flourished and are now scattered over much of the Interandean landscape, naturalizing themselves in such a way that the term forest, or *Bosque*, is now well-nigh synonymous with monospecific stands of *Eucalyptus* (Morris 1985). The introduction of the Monterey pine (*Pinus radiata*) in the 1960s, further modified the landscape at higher altitudes replacing native elfin forests. Exotics from Australia, Africa and North America now dominate the Tropandean landscape (Sarmiento 1987). It will do much good to start using native species, such as *Psidium*, to enhance ecosystem processes, such as seed dispersal, while offering humans usable marketable resources, such as edible fruits and fuelwood, to recuperate the region's lost landscape character.

Several reforestation projects using native Andean tree species have been undertaken (e.g., Spier & Biederbick 1980; CESA 1984; Brandbyge & Holm-Nielsen 1987), some through development aid (e.g., Galloway 1986; Loján 1990; Carlson & Añazco 1990). Programmes for resource management (e.g., Sands 1993), with emphasis on soil conservation, have misleadingly presented traditional crop associations and domesticated animals as indicators of diversity. Thus, their scope did not go beyond the forestry tradition of rent-seeking plantations, and did not consider the entire restoration of landscape's pattern and processes. There is a need for a landscape approach (Forman 1995; Zonneveld 1995) towards sustainable development of the Tropandean region.

Conclusions

To convert pasture to forest with the ability to compete with the grass species involved, it will be necessary to jump-start succession, but this will succeed only after the thick soil root-mats and overcasting tillers of tussock grasses are eradicated. For tropical montane forests in northwestern Ecuador, dispersal ecology can be used for pasture conversion if, and only if, encroaching tussock grasses are removed from the cleared area, where otherwise tree recruitment will often be only by ramets.

Caveat

Some Tropandean sites in Ecuador are examples of extinction-prone areas (Ashton 1992); I see them as examples of ecosystem recovery (Sarmiento 1995*a*). A secret well-kept from tourists is that most of those small reserves, even some national parks and other protected areas, are secondary growth and are undergoing increasing pressure from encroachment and poaching. National and provincial governments should link their development goals with the maintenance and recuperation of remnants of original veg-

etation as a priority in land-use planning, to prevent healthier areas from stresses that are now faced at agricultural frontiers. By providing economic vigour for restoration practices in deteriorated areas, the contribution for tropical landscapes conservation at large will be better served (Southgate & Clarke 1993; Goodland *et al.* 1993).

Embracing restoration for conservation as part of the national policy of economic development will ensure that sustainable activities, namely agroforestry, small-scale agriculture, ecotourism and landscape restoration, will provide rural people with alternatives for land degradation abatement and environmental amelioration (Hamilton 1990). Restoration ecology practices, such as land reclamation, vegetation recovery, reforestation, terracing, extermination of introduced species in key areas, alley cropping interspersed with such as natural wind breakers and hedges as corridors, are essential elements for enhancing seed dispersal of forest species into the pasture. However, in cases of *Setaria sphacelata* pastures, proactive grass removal should first be applied, allowing deflected succession to resume natural progression after the avoidance of competition.

Furthermore, following Western's (1989) view of rural landscapes, reserves must be considered parts of a bigger conservation system that includes the village, the agricultural lands and the sensitive natural areas in the Tropandean region. Legislative measures that check deforestation are required in the catchment basins of montane forests as well as mandatory exclusion of riparian corridors down-stream and selected whole watersheds away from 'development'. Cooperative, ecological planning by developers should stimulate international financial cooperation in order to both strengthen capabilities for sustainability and ameliorate environmental stresses (*sensu* Stadel 1991) in cultural landscapes at the village level.

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