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Strong effects of a plantation with *Pinus patula* on Andean subpáramo vegetation: a case study from Colombia

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Abstract

The effect of a pine plantation on a native subpáramo system in the Andes of Colombia (3100 m above sea level) was studied. The vegetation of an 8 year-old plantation with *Pinus patula* was compared to that of the surrounding native subpáramo. 59 plots made in the subpáramo vegetation contained 121 vascular plant species. These plots were classified into three subpáramo communities and one Andean scrub community. Sixty-four plots made in the pine plantation contained 76 vascular plant species and were subdivided into four classes of pine cover. With increasing pine cover, pine plantation plots tended to become less similar to the subpáramo communities. Habitat-specific subpáramo species tended to disappear with increasing pine cover. After controlling for the effects of environmental variables in a partial canonical correspondence analysis, pine cover had a significant impact on plant species patterns. It is concluded that afforestation with *Pinus patula* resulted in strong negative effects on diversity and composition of the subpáramo vegetation at the study site.

Resumen

Se realizó un estudio comparativo entre la vegetación de una plantación con *Pinus patula* con la del subpáramo en los alrededores de la plantación, a 3100 m de altura sobre el nivel del mar en los Andes de Colombia. En el subpáramo se hicieron 59 levantamientos en donde se registraron 121 especies de plantas vasculares. Estos levantamientos se clasificaron en tres comunidades herbáceas de subpáramo y una comunidad de bosque andino bajo. En la plantación se hicieron 64 levantamientos en donde se encontraron 76 especies de plantas vasculares. Los levantamientos en las plantaciones se clasificaron según clases de cobertura de *Pinus patula*. Entre más alta la cobertura de *Pinus patula* en los levantamientos en la plantacion, más baja la similaridad entre estos y los levantamientos en el subpáramo. Las especies del subpáramo que mostraron una especificidad de habitat alta mostraron la más baja persistencia en la plantación. Después de haber controlado por el efecto de variables ambientales en una ordinación canónica parcial, la cobertura de *Pinus patula* mostró un impacto significante en los patrones de especies. Se concluye que la aforestación con *Pinus patula* tiene una influencia negativa fuerte sobre la diversidad y la composición de la vegetación del subpáramo en el sitio de estudio.

Keywords: Native species; TWINSPAN; Canonical correspondence analysis; Partial ordination

1. Introduction

Páramos are high-altitude grasslands that occur in equatorial America between 3000 and 5000 m (Cuatrecasas, 1958; Cleef, 1981; Lauer, 1981). In most studies Neotropical páramos are stratified into three altitudinal belts: subpáramo with high component of shrubs, grass páramo, often dominated by species of *Calamagrostis* or *Chusquea*, and the so-called superpáramo, which typically consists of sparse herbs and lichens found below permanent snow. Because of the high degree of diversity and endemism of páramo plant

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species, the degradation of these ecosystems significantly threatens earth's biodiversity (Luteyn, 1992).

Patches of upper montane forests, dominated by *Polylepis*, occur at altitudes up to 3500–4000 m above sea level (Fjeldså and Kessler, 1996). For this reason, discussion exists to which extent páramo grasslands should be considered former forest lands or natural grasslands (Laegaard, 1992; Wille et al., 2002). The first interpretation yields arguments in favour of afforestation of páramo areas with exotics, in particular when the positive effects of plantation forests upon biodiversity restoration are considered (Morris, 1997). In the context of forest ecosystem rehabilitation (Lugo, 1992; Clüsener-Godt and Hadley, 1993), planting of alien tree species is reported to favour regeneration of secondary forest species (Parrotta, 1992, 1995), leading to increased diversity levels in comparison with unforested control sites. Management of plantation forests (e.g. applying adequate planting distances, thinning, and selection of tree species) may influence the degree of colonization of native understorey species (Guariguata et al., 1995; Harrington, 1999). Cavelier and Tobler (1998) showed that 21-year-old abandoned plantations of *Pinus patula* and *Cupressus lusetanica*, still supported only a small fraction of the native natural montane forest at 2000 m above sea level in the northern Andes of Colombia.

The second interpretation (páramo grasslands considered as natural grasslands) directs research to questions how the natural páramo system is affected by planting alien species. This issue has gained importance in the area of the high plain of Bogotá, where the impact on biodiversity and hydrology of recent afforestation programmes with species of *Acacia* and *Pinus* by the Corporación Autónoma Regional de Cundinamarca'' (CAR) is currently under evaluation (Van der Hammen, 1998). It is widely known that planting of pines in native non-forest vegetation types strongly alters soil characteristics and eventually can reduce plant diversity (e.g. N'zala et al., 1997; Welch and Scott, 1997; Scholes and Nowicki, 1998). Yet, in a regional study carried out in the Ecuadorian Andes, Hofstede et al. (2002) reported that vegetation under pine plantations was quite similar to extensively grazed páramo grasslands. In Colombia, four species of *Pinus* (*P. patula*, *P. radiata*, *P. oocarpa*, and *P. caribaea*) are used in plantation forestry (Bartholomäus et al., 1998). *Pinus patula* or Mexican weeping pine is native to the Sierra Madre Oriental in Mexico (Perry, 1991; Richardson and Rundel, 1998) and is well adapted to the physiographic and climatic conditions of the high Andean zone (Jongsma, 1998). The current study intended to evaluate in a local setting (a mountain ridge near Guatavita in the High plain of Bogotá) the effects of a plantation with *Pinus patula* upon diversity and composition of plant communities in an adjacant native Andean subpáramo. Care was taken to minimise habitat differences between the studied subpáramo and the plantation. Specifically, the research addressed the question how the similarity in plant diversity and composition between the subpáramo communities and the vegetation in the pine plantation changed as a function of pine cover.

2. Methods

2.1. Location and plantation history

The research area is part of the Cerro de Esmeralda mountain ridge (approximately 4° 55′ N, 73° 50′ W), located near Guatavita, 40 km north of Bogotá, Colombia. This ridge is built up by the Guadalupe Formation, which dates from the Upper-Cretaceous and consists at the research site of compact friable sandstone with intercalations of siltstone and claystone (Helmens, 1990). The research site is located near the flat summit of the ridge, between 3000 and 3100 m above sea level. The annual precipitation near the summit area is about 800 mm and shows, on average, a bimodal yearly distribution with peaks from March to May, and October to November (records from 1941 to 2001 supplied by the CAR, climatic station of Guatavita at 2625 m above sea level).

Afforestation was executed by the CAR in 1991, applying a uniform planting density of 3×3 m in the entire plantation. At the time of the field work (in 1999) for the study here presented, the 8-year old planted pine trees reached a height of approximately 6 m. No thinning or harvesting of the pine trees had occurred, and the density of planted pines did not change markedly from the initially applied planting density. The plantation covers an area of several tens of hectares. It is surrounded by relatively dry scrubby subpáramo vegetation, which, at places, merges into a low (height 2–3 m) Andean scrub forest (hereafter the term ''subpáramo'' includes Andean scrub forest, unless otherwise indicated). Our own observations and oral records from the landowner confirm the presence of natural subpáramo vegetation in the plantation area at the time of afforestation, with habitat conditions similar to those in the subpáramo surrounding the current plantation area. There were no indications that the subpáramo had been recently burned, grazed, or otherwise disturbed before afforestation activities. During the fieldwork, no dung was discovered, indicating the absence of cattle.

2.2. Data collection

The vascular plant composition of the natural subpáramo and the pine plantation was studied by means of 123 plots, 59 of which were situated in subpáramo vegetation and 64 in the pine plantation. Prior to plot sampling, the plantation and subpáramo area was subjectively subdivided in patches with visually homogeneous vascular plant species composition and vegetation structure. Plots were randomly located in these patches. The nearest distances between plots varied from approximately 4–50 m. Plots were square or rectangular, and varied in size from 1 to 12 m^2. Plot size and shape were chosen to minimise sampling effort while including in the plots all vascular plant species observed in the patch. In each plot the vertical projection onto the soil surface of the aboveground living phytomass above the plot area was visually estimated. In addition, the cover of bare mineral soil, rocks and stones, lichens, mosses, and pine litter was estimated. The cover in these estimates was expressed as percentage of the plot area. The identification of the plant species was carried out at the National Herbarium of Colombia in Bogotá (COL). Some plants could only be identified at the level of family or genus. Plant species names and their authorities are according to Luteyn (1999).

In each plot, soil samples were taken at five randomly chosen points at 10–15 cm depth after removing the ectorganic horizons. After having cleared the samples from roots, the five subsamples were combined into one bulk sample. Organic matter content was determined by loss on ignition (Allen et al., 1974). In this procedure, samples were dried at 105 °C for 12 h to remove all soil bound water (H_2O) and were subsequently ignited at 400 °C for 16 h to oxidise all organic matter. Differences before and after ignition are given as % loss of dry weight (105 °C). For preparation of all other analyses, the soil samples were dried at 60 °C for 12 h. Dried subsamples were suspended in deionised water at a ratio of 1:5 and shaken for 2 h, in order to measure pH and electro-conductivity (EC). In the same extractions, phosphate (PO_4) concentrations were measured colorimetrically with an autoanalyser (Technicon II™), potassium (K) concentrations using an atomic absorption spectrophotometer (Perkin-Elmer 1100B™). Soil analyses took place at the Institute for Biodiversity and Ecosystem Dynamics of the Universiteit van Amsterdam.

2.3. Data analysis

The plots made in the natural vegetation were classified by means of TWINSPAN (Hill, 1979), applying default entries except for the selection of only one cut level (0). First-order jackknife estimates of species richness were calculated for each vegetation class (Manly, 1997). These estimates perform relatively well to approximate community species richness on the basis of plot samples (Palmer, 1991). The similarity between the native subpáramo communities and each individual pine plantation plot was determined using the Sørensen coefficient (Magurran, 1988). This coefficient is calculated as follows:

$$Cs = 2j/(a + b)$$

in which Cs = Sørensen similarity coefficient; j = the number of species found at both sites; a = the number of species found at site A; b = the number of species found at site B. *Pinus patula* was excluded from all pine plantation plots in these comparisons.

Principal component analysis (PCA) of soil chemical data was carried out using SYSTAT 5.2 (1990). Some variables were log transformed to reduce skewness. Spearman correlation coefficients were calculated between altitude, soil depth, and pine cover of the plantation plots. Canonical correspondence analysis (CCA) was performed using CANOCO 4.0 (Ter Braak and Smilauer, 1998), using presence–absence data of species, with a scaling focus on inter-sampling distances, and with Hill's scaling type. Variance inflation factors of the environmental variables were below 1.5. A permutation test was done with 199 permutations under reduced model to examine the significance of the canonical axis of the partial CCA. In these ordination analyses, *Pinus patula* was excluded from the floristic plot data.

3. Results

3.1. Classification

The plots in the natural subpáramo vegetation covered a total sampling area of 178 m^2, and included 121 vascular plant species. The TWINSPAN classification resulted in four clusters of plots (Table 1): one Andean scrub forest (type I) and three subpáramo communities (types II–IV). Community I (*Macleania rupestris–Oreopanax* community) was based on 12 plots which contained 80 species. This community occurred on a relatively dry slope. However, conditions under the rather dense canopy were quite moist and the moss layer was well developed. Epiphytic bromeliaceous species were fairly abundant. Community II (*Myrica parvifolia–Weinmannia tomentosa* community) was based on eight plots containing 63 species, and represented the transition between the Andean scrub forest and the subpáramo. Patches covered by *Weinmannia tomentosa* appeared at open and windy spots, often near the mountain ridge. Other patches were dominated by *Myrica parvifolia* and occurred in more sheltered parts. Community III (*Miconia andina–Paepalanthus* aff. *columbiensis* community) represented a subpáramo vegetation dominated by dwarf shrubs, grasses, herbs and stem rosettes of *Espeletiopsis corymbosa*. This vegetation type was based on 28 plots containing 75 species and was found near the summit of the ridge.

Table 1
List of vascular plant species found in this study[a]

	Subpáramo communities				Pine plantation categories			
	I	II	III	IV	0%	>0 to 40%	>40 to 80%	>80 to 100%
Compositae sp. BW105	42	13	0	9	0	0	0	0
Xylosma spiculiferum Triana & Planch.	8	0	0	0	0	0	0	0
Viburnum triphyllum Benth.	25	0	0	0	0	0	0	0
Stevia lucida Lag.	17	0	0	0	0	0	0	0
Iridaceae sp. BW116	8	0	0	0	0	0	0	0
Hypericum sp. BW122	8	0	0	0	0	0	0	0
Gramineae sp. 1	58	13	0	0	0	0	0	0
Dendrophthora clavata (Benth.) Urb.	33	0	0	0	0	0	0	0
Compositae sp. BW120	17	0	0	0	0	0	0	0
Compositae sp. BW114	8	0	0	0	0	0	0	0
***Cestrum* sp. 1**	8	0	0	0	4	7	0	0
***Cavendishia cordifolia* (Kunth) Hoerold**	17	0	0	0	9	7	0	0
Baccharis tricuneata (L. f.) Pers.	8	0	0	0	0	0	0	0
Baccharis bogotensis Kunth	8	0	0	0	0	0	0	0
Achyrocline bogotense (Kunth) DC.	17	0	0	0	0	0	0	0
***Vallea stipularis* Mutis ex L. f.**	67	0	4	0	4	0	0	0
***Symplocos* sp. BW176**	67	13	7	0	4	0	0	0
Rubiaceae sp. BW119	25	0	0	0	0	0	0	0
Oreopanax sp. 1	33	0	0	0	0	0	0	0
***Myrcianthes leucoxyla* (Ortega) McVaugh**	83	13	0	0	4	7	0	0
***Monnina salicifolia* Ruiz & Pav.**	42	0	4	0	9	7	0	0
***Berberis* cf. *rigidifolia* Kunth**	75	13	4	0	9	0	0	0
Myrsine guianensis Aubl.	17	0	0	0	0	0	0	0
Pteridaceae sp. BW121	17	0	0	0	0	0	0	0
Orchidaceae sp. BW008	8	0	0	0	0	0	0	0
Orchidaceae sp. BW006	75	25	4	0	0	0	0	11
Orchidaceae sp. BW001	8	0	0	0	0	0	0	0
Bromeliaceae sp. BW113	42	13	0	0	0	0	0	0
Bomarea caldasiana Herb.	25	0	0	0	0	0	0	0
Asclepidaceae sp. BW172	17	0	0	0	0	13	0	0
Ageratina gracilis (Kunth) R.M. King & H. Rob.	75	25	0	9	0	0	0	0
Acrostichiaceae sp. BW129	25	13	0	0	0	0	0	0
Rubiaceae sp. BW133	58	25	4	0	9	0	0	0
Niphogeton sp. BW103	17	13	0	0	0	0	0	0
***Hesperomeles goudotiana* (Decne.) Killip**	92	50	4	9	9	13	0	0
Diplostephium revolutum S.F. Blake	67	25	7	0	0	0	0	0
***Symplocos* sp. BW102**	83	75	4	0	13	0	0	0
***Smilax tomentosa* Kunth**	75	63	4	9	22	7	0	0
Miconia sp. BW137	67	50	4	9	0	0	0	0
Eryngium humboldtii F. Delaroche	8	13	0	0	0	0	0	0
Bromeliaceae sp. BW111	92	63	4	0	13	7	0	0
***Palicourea* sp. BW150**	8	13	0	0	9	7	0	0
Orchidaceae sp. BW107	17	13	0	0	0	0	0	0
***Macleania rupestris* (Kunth) A.C. Sm.**	92	63	11	0	30	13	0	0
Compositae sp. BW104	50	38	0	0	0	7	0	0
Caryophyllaceae sp. BW132	8	13	0	0	0	0	0	0
Bromeliaceae sp. BW112	58	38	7	0	4	0	0	0
***Rhamnus goudotiana* Triana & Planch.**	42	50	7	0	22	7	13	0
Orchidaceae sp. BW003	50	50	7	9	0	0	0	0
***Myrica parvifolia* Benth.**	83	75	18	9	22	33	25	11
Ageratina cf. *viscosa* (Kunth) R.M. King & H. Rob.	17	25	4	0	0	0	0	0
***Weinmannia tomentosa* L. f.**	0	38	4	0	9	0	0	0
Senecio sp. 1	0	13	0	0	0	0	0	0
Pteridaceae sp. BW151	0	13	0	0	0	0	0	0
Peperomia sp. BW126	0	13	0	0	0	0	0	0
Compositae sp. BW128	0	13	0	0	0	0	0	0
***Miconia squamulosa* (H. Karst.) Triana**	17	0	4	0	0	0	13	0
***Diplostephium rosmarinifolius* (Benth.) Wedd.**	17	13	4	0	9	0	0	0

(*continued on next page*)

Table 1 (*continued*)

	Subpáramo communities				Pine plantation categories			
	I	II	III	IV	0%	>0 to 40%	>40 to 80%	>80 to 100%
Acrostichiaceae sp. BW115	17	13	4	0	0	0	0	0
***Pernettya hirta* (Willd.) Sleumer**	83	88	36	9	35	13	13	6
***Miconia summa* Cuatrec.**	58	63	25	9	35	7	13	6
***Bucquetia glutinosa* (L. f.) DC.**	42	50	25	18	43	40	13	11
***Ageratina* sp. BW145**	50	50	25	0	17	13	13	28
Masdevallia coriacea Lindl.	8	13	7	0	0	0	0	0
***Rhynchospora oreoboloidea* Gómez-Laur.**	8	0	4	9	4	0	0	0
***Rhynchospora macrochaeta* Steud. ex Boeck.**	50	38	50	45	43	53	38	33
***Paspalum bonplandianum* Flügge**	58	25	39	36	26	40	25	11
***Hieracium* cf. *avilae* Kunth**	8	0	4	9	13	0	0	0
***Muehlenbeckia tamnifolia* (Kunth) Meisn.**	8	13	0	18	0	0	0	17
***Hypericum juniperinum* Kunth**	25	13	7	55	0	0	13	0
***Castilleja* sp. 1**	17	0	21	45	0	7	0	0
Pteridium aquilinum (L.) Kuhn	0	13	4	0	0	0	0	0
***Epidendrum chioneum* Lindl.**	8	38	18	0	13	7	0	0
Gramineae sp. BW139	42	0	39	55	13	7	0	0
Gramineae sp. BW136	0	25	14	45	43	60	50	28
***Arcytophyllum nitidum* (Kunth) Schltdl.**	50	88	82	91	70	60	63	17
Gramineae sp. BW135	17	50	68	45	13	40	0	17
***Cortaderia planifolia* Swallen**	17	50	71	9	52	27	38	11
***Puya* sp. BW165**	0	38	29	0	4	13	13	6
***Puya lineata* Mez**	0	25	29	36	0	7	0	0
***Lycopodium thuyoides* Humb. & Bonpl. ex Willd.**	42	38	71	0	48	67	38	17
***Gaultheria erecta* Vent.**	33	38	64	55	30	33	25	6
Elaphoglossum sp. BW153	8	25	25	9	0	0	0	0
***Clethra fimbriata* Kunth**	17	13	29	9	39	33	13	6
Centropogon* aff. *sphaerogynia	25	63	75	55	43	47	25	22
***Brachyotum strigosum* (L.f) Triana**	0	38	29	0	17	13	13	6
Pleurothallis sp. BW009	0	0	4	0	0	0	0	0
Orchidaceae sp. BW004	0	0	4	0	0	0	0	0
Lycopodiaceae sp. BW143	0	0	7	0	0	0	0	0
***Bejaria resinosa* Mutis ex L. f.**	8	0	29	9	9	33	0	0
***Gaylussacia buxifolia* Kunth.**	8	0	32	9	13	13	13	0
Elleanthus sp. BW002	0	0	4	0	0	0	0	0
***Lycopodium contiguum* Klotzsch**	8	0	36	0	35	33	38	0
***Sisyrinchium* sp. 1**	0	0	7	0	9	0	0	0
***Puya* sp. BW177**	0	0	4	0	4	0	0	0
***Miconia andina* Naudin**	0	0	36	0	35	33	50	17
Lupinus bogotensis Benth.	0	0	4	0	0	0	0	0
Cyperaceae sp. BW149	0	0	29	9	9	27	0	0
***Paepalanthus* aff. *columbiensis* Ruhland**	0	13	93	91	96	87	75	50
***Hypericum tetrastichum* Cuatrec.**	0	0	57	73	35	53	13	0
***Espeletiopsis corymbosa* (Bonpl.) Cuatrec.**	0	38	75	55	39	60	50	17
Gramineae sp. BW138	0	0	4	9	22	13	13	0
***Vaccinium floribundum* Kunth**	0	0	4	9	4	0	0	0
Melastomataceae sp. BW130	0	0	4	9	4	0	0	0
Lobelia tenera Kunth	0	0	4	9	0	0	0	0
***Chaetolepis microphylla* (Bonpland) Miq.**	0	13	39	82	35	47	13	6
Gramineae sp. BW140	0	0	4	18	39	13	13	6
Ditassa caucana Pittier	0	0	4	18	0	0	0	0
***Achyrocline crassipes* (S.F. Blake)**	0	0	4	27	13	27	0	6
***Stenorrhynchos vaginatum* (Kunth) Spreng.**	0	0	0	9	17	7	0	0
***Noticastrum marginatum* (Kunth) Cuatrec.**	0	0	0	64	4	13	0	0
***Lourteigia* cf. *microphylla* (L. f.) R.M. King & H. Rob.**	0	0	0	55	9	7	0	0
Hypochaeris radicata L.	0	0	0	18	0	0	0	0
***Hypericum mexicanum* L.**	0	0	0	36	9	7	25	0
Gramineae sp. BW134	0	0	7	45	4	0	0	0
Gramineae sp. BW123	0	0	0	18	0	13	13	22
***Bulbostylis* cf. *glaziovii* (Boeck) C.B. Clarke**	0	0	11	64	17	7	13	0

(*continued on next page*)

Table 1 (*continued*)

	Subpáramo communities				Pine plantation categories			
	I	II	III	IV	0%	>0 to 40%	>40 to 80%	>80 to 100%
***Achyrocline alata* (Kunth) DC.**	0	13	0	73	0	7	0	0
***Acaena cylindristachya* Ruiz & Pavon**	0	0	0	18	0	13	0	0
Pentacalia vaccinioides (Kunth) Cuatrec.	8	0	7	27	0	0	0	0
Agrostis sp. BW158	0	13	0	27	0	0	0	0
—underlying species were only recorded in plantation plots								
Orchidaceae sp. BW. 000	0	0	0	0	0	7	0	0
Sporobolus lasiophyllus Pilger	0	0	0	0	0	7	13	0
Acacia decurrens Wildd.	0	0	0	0	0	7	0	0
Pinus patula Schiede ex Schltdl. & Cham.	0	0	0	0	0	100	100	100

[a] Species and plots from the native subpáramo vegetation are grouped according to the TWINSPAN classification. Species encountered in both pine plantation and native subpáramo vegetation are in bold type-face. Values indicate frequency in% (number of plots in which species are recorded divided by total number of plots in each vegetation class).

Community IV (*Noticastrum marginatum–Chaetolepis microphylla* community) was a rocky subpáramo community that consisted of dwarf shrubs and small herbaceous species. This type was sampled in 11 plots containing 53 species and was situated on rock substrates, which showed a patchy distribution in the subpáramo.

The pine plantation plots covered a total sampling area of 203 m^2 and contained 76 vascular plant species (Table 1). These plots were grouped into four classes of increasing cover of *Pinus patula* (Fig. 1). Class 0% consisted of 23 plots that were located inside the plantation, but where *Pinus patula* had zero aboveground cover. In these plots, which can be seen as small gaps in the middle of the pine plantation, 61 vascular plant species were found. In the other three categories the pine cover was >0 to 40% (15 plots), >40 to 80% (eight plots), and >80 to 100% (18 plots). The numbers of vascular plant species in these categories were 57, 33, and 27, respectively.

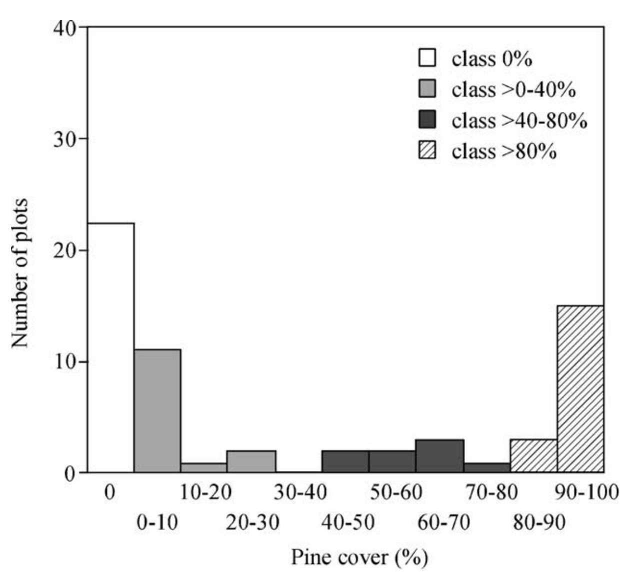

Fig. 1. Frequency diagram of pine cover values in the plantation plots, which are subdivided into four classes of pine cover categories.

3.2. Comparison between subpáramo and pine plantation vegetation

Even though the overall soil and habitat conditions of native subpáramo and plantation area were found similar at the time of afforestation, the plots in rock subpáramo (IV) showed substantially more rock outcrop and shallower soils than found in the plantation plots. Also, six plots from the subpáramo community (III) had considerably shallower soils (soil depth $\leqslant 5$ cm) than recorded in the plantation area. Five plots in the Andean scrub community (I) were made at altitudes below 3050 m, which was outside the altitudinal range of the plantation plots. In order to minimise soil and habitat differences between the plots from the native subpáramo vegetation and the plantation, all these plots were deleted from further analyses.

The jack-knife species richness of the plantation plots with low pine cover (pine cover categories 0 and >0 to 40%) was about similar to that of the native subpáramo. However, in the clusters of plantation plots with higher pine cover the estimated species richness decreased to 42% of the native subpáramo communities (Table 2). The plant species composition of the plantation plots arranged in pine cover classes was compared to the composition found in the individual subpáramo plots (Fig. 2) and in the subpáramo communities as a whole (Table 3). In both comparisons, the vegetation in the pine plantation tended to become less similar to the subpáramo vegetation when pine cover increased. Remarkably, the pine plantation hardly contained any non-páramo species. Apart from *Pinus patula* only *Acacia decurrens* (an exotic tree species used in plantation forestry in the wide surroundings of the study site), and two herbaceous species (*Sporobolus lasiophyllus* and

Table 2
Properties of plots used in the comparison between subpáramo and plantation

	Native subpáramo communities			Plantation pine tree cover categories			
	Andean scrub (I)	Transitional (II)	Subpáramo (III)	0%	>0 to 40%	>40 to 80%	>80 to 100%
Soil chemical properties at 10–15 cm							
pH	4.0 (0.3)	4.0 (0.2)	4.3 (0.3)	4.5 (0.3)	4.5 (0.22)	4.5 (0.2)	4.6 (0.2)
EC	133 (39.9)	132 (27.5)	71 (23.0)	61 (31.5)	57 (13.0)	64 (19.4)	60 (29.1)
Organic matter content (%)[a]	42.9 (23.0)	25.7 (18.2)	13.1 (5.1)	10.0 (7.3)	10.6 (9.5)	11.9 (5.7)	17.3 (17.3)
PO_4 mg kg^{-1} [a]	0.4 (0.4)	0.3 (0.2)	0.2 (0.2)	0.4 (0.2)	0.3 (0.2)	0.3 (0.2)	0.3 (0.3)
K mg kg^{-1} [a]	36.9 (19.6)	33.1 (9.8)	23.0 (8.8)	13.6 (8.3)	12.0 (2.8)	12.9 (3.9)	13.0 (5.7)
Cover (%) at soil surface of							
Bare mineral soil visible	0.0	0.1 (0.2)	1.4 (1.5)	7.9 (21.0)	4.4 (8.2)	0.4 (0.4)	0.4 (1.1)
Rocks and stones at surface	0.0 (0.0)	0.7 (1.8)	5.4 (9.9)	0.4 (1.5)	0.0 (0.0)	1.2 (2.7)	0.1 (0.2)
Lichens (on mineral material)	4.2 (4.1)	1.9 (1.7)	3.6 (6.1)	2.8 (4.9)	0.8 (0.7)	0.7 (1.0)	0.4 (0.9)
Lichens (on necromass)	33.4 (20.6)	10.6 (13.7)	2.3 (4.4)	5.8 (16.0)	0.5 (1.4)	0.1	0.0
Mosses (on mineral material)	38.7 (19.0)	23.7 (31.2)	4.8 (4.0)	3.6 (4.5)	3.8 (3.9)	1.0 (0.7)	0.7 (1.1)
Mosses (on necromass)	3.2 (3.5)	0.5 (1.0)	0.0	0.0	1.3 (4.1)	0.0	0.0
Pine litter visible at surface	0.0	0.0	0.0	16.3 (23.8)	28.0 (34.2)	80.6 (24.7)	86.3 (28.5)
Other properties							
Mineral soil depth in cm	32.9 (19.8)	47.5 (28.7)	37.7 (31.7)	62.6 (26.8)	61.3 (30.4)	70.0 (20.7)	75.6 (23.3)
Depth ectorganic horizon in cm	17.1 (9.1)	18.4 (9.6)	2.7 (4.0)	5.1 (4.0)	10.7 (5.9)	9.3 (4.5)	14.3 (6.7)
Altitude in m above sea level	3054 (2)	3067 (14)	3078 (5)	3070 (6)	3067 (8)	3066 (8)	3062 (8)
Jack-knife species richness[b]	83 (8)	87 (17)	74 (6)	72 (16)	77 (22)	48 (12)	35 (12)
Plot size (m^2)	6.3 (2.9)	4.0 (0.0)	3.0 (1.4)	3.1 (2.4)	4.1 (1.5)	4.0 (0.0)	1.6 (1.3)
Total area sampled (m^2)	44	32	66	74	62	32	36
Number of plots (N)	7	8	22	23	15	8	18

Shown are the averages of plots arranged according to vegetation class, with standard deviations between parentheses.
[a] Log transformed before PCA.
[b] Excluding *Pinus patula*.

an orchid, see Table 1) were recorded in the plantation plots.

The native subpáramo species were subdivided in three categories of habitat specificity (ecological amplitude), according to their presence in the three remaining native subpáramo communities. Broad, medium, and narrow amplitudes corresponded to a presence in 3, 2, and 1 native communities, respectively. Classified in this way, habitat-specific subpáramo species (with narrow ecological amplitude) tended to show the lowest persistence in the pine plantation (Fig. 3). In pine plantation plots with increasing pine cover, these species tended to disappear. The least habitat-specific subpáramo species (with broad ecological amplitude) persisted better in the pine plantation.

Canonical correspondence analysis of subpáramo and pine plantation plots together was carried out to

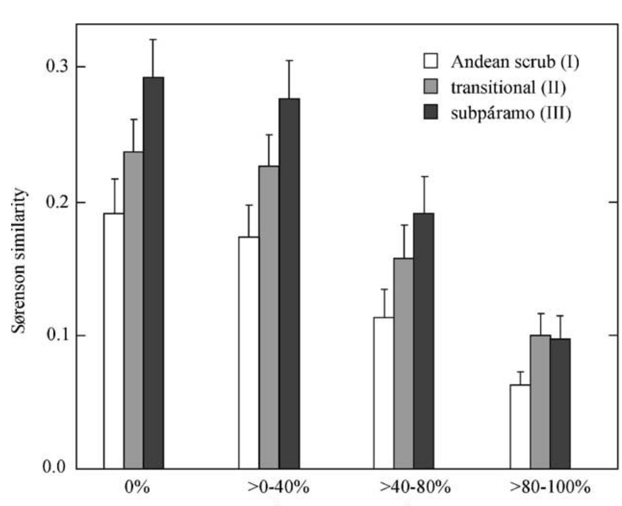

Fig. 2. Sørenson similarity coefficients between individual plots of the pine plantation and the native subpáramo communities. Shown are average similarity (bars) and one standard deviation.

Table 3
Sørenson similarity coefficients between the native subpáramo communities and the pine plantation plots arranged according to pine cover classes

	Pine cover classes			
	0%	>0 to 40%	>40 to 80%	>80 to 100%
Andean Scrub (I)	0.56	0.48	0.37	0.33
Transitional (II)	0.56	0.52	0.44	0.49
Subpáramo (III)	0.80	0.65	0.59	0.52

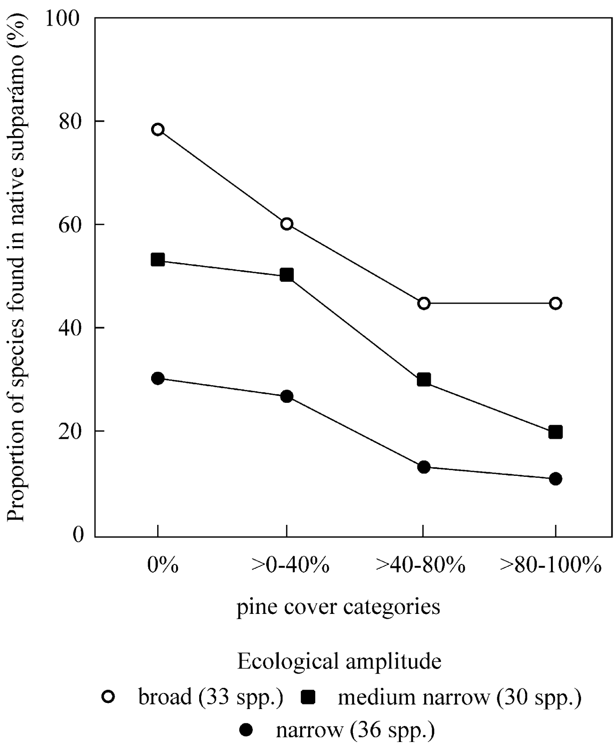

Fig. 3. The relative amount of native subpáramo plant species found in the pine plantation plots grouped according to pine cover.

separate the effect of pine cover on floristic composition from that of soil depth, altitude, and soil chemical information. Principal component analysis was applied to reduce the chemical soil data into two components. The first PCA axis explained 64%, and was mostly correlated with potassium concentration, EC, pH, and organic matter content (loadings of 0.94, 0.93, −0.86, and 0.78, respectively). The second PCA axis explained only 20%, and was mostly correlated with P (the loading for P was −0.91 while the other loadings were below 0.37). Pine cover was slightly positively correlated with soil depth (Table 4), which was partially due to the somewhat deeper soils in the plantation plots compared with the native subpáramo plots (Table 2). Pine cover was negatively associated with altitude, which may be due to the comparatively high location of the plots in the subpáramo community (III) and the plantation pine category of 0% (Table 2). The slightly negative correlation between pine cover and the first PCA axis seemed due to the EC, high organic matter content, and K levels in the Andean scrub (I) and transitional subpáramo (II) communities (Table 2). Because of these correlations the effect of pine cover on patterns of diversity and composition could not be separated entirely from the effects of the other environmental variables.

Table 4
Spearman correlation coefficients between the environmental variables used in the canonical ordination analyses

	Pine cover	Soil depth	Altitude	PCA axis1
Soil depth	0.38			
Altitude	−0.36	−0.43		
PCA axis1	−0.39	−0.44	0.15	
PCA axis2	−0.04	0.19	−0.23	0.02

Plant species patterns were mostly influenced by the first PCA axis and altitude (Tables 5 and 6), resulting in the separation of plots from the Andean scrub páramo (I) and the transitional subpáramo (II) towards the positive side of the first CCA axis (Fig. 4). Pine cover and soil depth governed species patterns along the second CCA axis, mostly separating plantation plots with high pine cover from the rest of the plots.

After controlling for the effects of four environmental variables in a partial CCA, pine cover had a significant impact on plant species patterns (permutation test of canonical axis: F-ratio 1.8, $P = 0.01$; see also Table 5). All plantation plots of the two highest pine cover categories were separated from the remaining plots (Fig. 5). The species composition in the plantation plots that were separated along the first axis was clearly influenced by the pure (environment-controlled) pine cover. The separation of the plantation plots along the second axis was due to residual effects most likely related to the presence of the pines in or near these plots, but not related to aboveground cover estimates of the pines, or to the supplied environmental factors. The plantation plots in the low pine cover categories were hardly separated from the subpáramo plots in the partial ordination diagram. The most likely explanation for this is that the effect of low pine cover on the species composition in the plantation plots was fully accounted for by the supplied environmental factors.

4. Discussion

The results of this case study strongly suggest that 8 years after afforestation with *Pinus patula* the diversity and composition of the subpáramo vegetation at the Cerro de Esmeralda Mountain changed severely. Species diversity in the afforested subpáramo decreased with increasing pine cover, and floristic composition showed a comparatively strong loss of habitat-specific subpáramo species. These latter species presumably hold much of ecological and scientific value of the subpáramo ecosystem. Reports on differential responses of native plant species to pine plantings are rare. Michelsen et al. (1996) found that most of the understorey herbs in Ethiopian highland plantations of *Pinus*, *Eucalyptus* and other exotic tree taxa were widespread. This might correspond to the loss of páramo specialists in the current study, considering that wide distributions of species can be attributed to a low degree of ecological

Table 5
(A) Summary of the CCA; (B) summary of the partial CCA, with soil depth, altitude, PCA axis1, and PCA axis2 as covariables

	axis 1	axis 2	axis 3	axis 4	Total inertia
(A)					
Eigenvalues	0.40	0.18	0.11	0.11	6.62
Cumulative percentage variance of species data	6	8.7	10.4	12	
Sum of all unconstrained eigenvalues					6.62
Sum of all canonical eigenvalues					0.87
(B)					
Eigenvalues	0.11	0.44	0.25	0.23	6.62
Cumulative percentage variance of species data	1.9	9.5	13.8	17.7	
Sum of all unconstrained eigenvalues					5.86
Sum of all canonical eigenvalues					0.11

Table 6
Canonical regression coefficients and intraset correlation coefficients of the CCA

	Regression coefficients		Intraset correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Pine cover	−0.091	0.24	−0.19	0.64
Soil depth	0.033	0.21	−0.18	0.72
Altitude	−0.47	−0.13	−0.73	−0.46
PCA axis1	0.53	−0.08	0.79	−0.42
PCA axis2	0.12	0.19	0.30	0.38

specialisation (generalist species would be able to exploit a wider range of resources and show less habitat specialisation; see more explanations of abundance–distribution relationships in Gaston and Kunin, 1997). Welch and Scott (1997) reported a strong decline of shade-tolerant understorey plant species in a 20-year-old pine plantation in England. They predicted that colonisation would be the main factor limiting further development of understorey plant diversity in the plantation.

The higher the pine cover in plantation plots, the lower the floristic similarity between these and the native subpáramo vegetation. It suggests that pine trees may be able to outcompete many subpáramo species due to their high growth rate (Perry, 1991; Richardson and Rundel, 1998), more efficient nitrogen uptake (Northup et al., 1995; Read, 1998), and the changes in soil organic matter and soil nutrient cycling induced by pine litter (Scholes and Nowicki, 1998; Dames et al., 1998). The native subpáramo species that withstand increasing pine cover, especially those with a broad ecological amplitude in this study, might have a high tolerance for shady conditions and pine litter, or show a high ability to compete for nutrients and water with belowground pine roots. Conversely, the species with small ecological amplitude that disappear might be most sensitive for light interception, the changing soil conditions and the increased amount of pine roots. Even when pine trees had no cover and were only found in the immediate surroundings of the plantation plots, these plots lacked almost two-third of the most typical habitat-specific subpáramo species. This result suggests that simply the opening-out of the canopy of a developing pine stand (either by thinning measures or by natural processes) mostly induces settlement or persistence of habitat-indifferent native subpáramo species with relatively low intrinsic value. However, it should be borne in mind that the pine planting density was uniformly applied at times of afforestation at the study site. Apart from phytosanitary factors, the gaps in the pine stands might be due to unfavourable habitat conditions for growth or survival of the young pines. Such factors may also have had a negative influence on native subpáramo species in these gaps.

The strong altitudinal effect on the species patterns in the canonical ordination is remarkable in view of the narrow altitudinal range of the plot locations. Partially this is due to the fact that the study site was near the assumed natural upper forest line in the Andes (Wille et al., 2002), which is, among others, related to plant responses to frost (Körner, 1998). In the central parts of the eastern cordillera in Colombia, the transition zone between Andean montane forest and subpáramo on mountain ridges (top effect) is often positioned somewhere

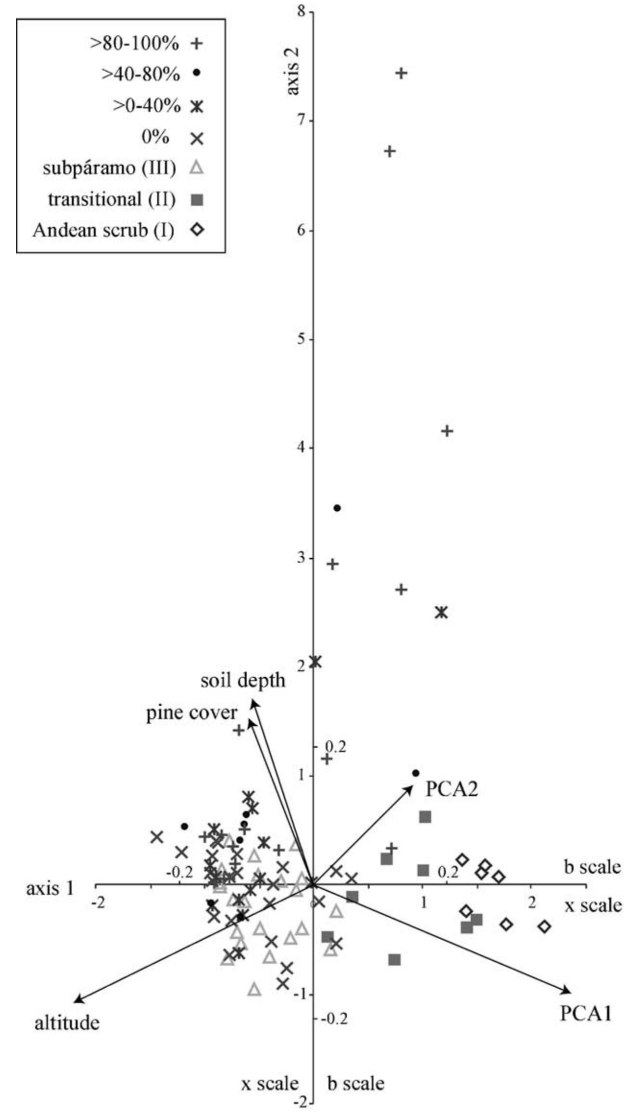

Fig. 4. CCA ordination diagram showing plot scores (symbols) derived from the species, and biplot scores of environmental variables (vectors). The *b* scale applies to the environmental variables and the *x* scale to the plots. See ordination results in Table 5.

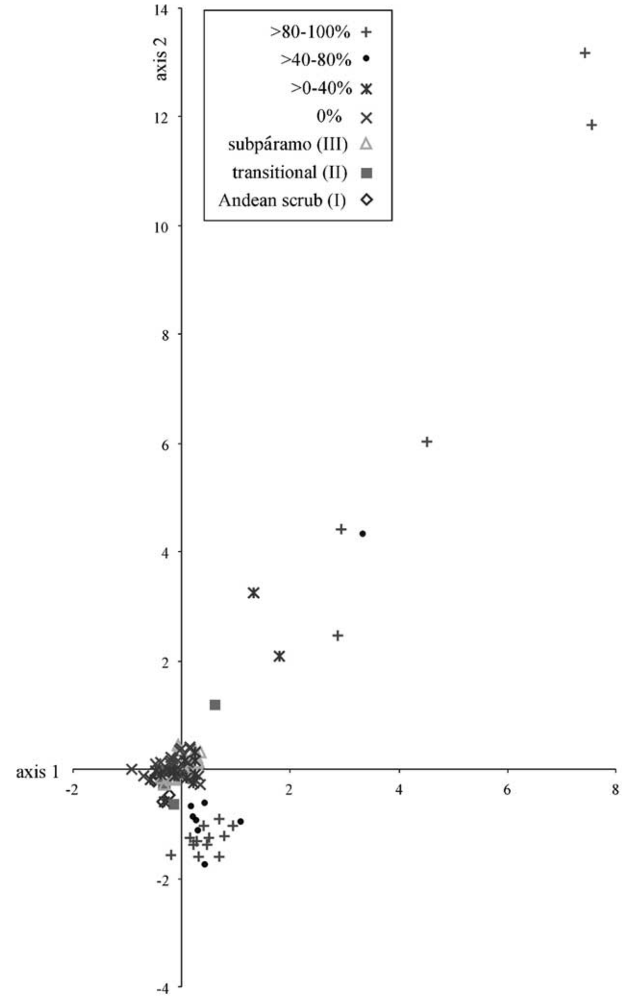

Fig. 5. Partial ordination diagram showing plot scores (symbols) derived from the species, after partialling out the effects of altitude, soil depth, soil PCA1 and soil PCA2. The first axis is a partial CCA axis and shows the plot scores constrained to be a linear combination of the pine cover. The second axis is a partial CA axis. See ordination results in Table 5.

near 3000 m above sea level (Cleef, 1981). Slight differences in altitude along this mountain forest line may have relatively strong effects of plant performances. The altitudinal effect may also be due to the topography of the study site, which is situated near the summit of a mountain ridge. Usually, along such summit areas, catenary soil sequences are well developed, resulting in truncated soils at upslope zones and deeper soils with colluvial enrichment down the slopes. These conditions were likely present in the study area as shown by the negative correlations between altitude and soil depth, as well as the first PCA axis of the chemical soil information (Table 2). Also, the summit area of the ridge was more exposed to wind and rain compared to downslope areas where incipient valley systems buffered against hostile weather influences.

Due to the correlation between the environmental factors and pine cover estimates, the ordination results were less conclusive than the comparative similarity study (Table 3 and Figs. 2 and 3), with respect to the impact of pine in low aboveground cover. Only in the plots with high pine cover, the pure effect of pines was strong enough to become apparent. As a whole, the clear negative control of pine trees on plant species patterns in the subpáramo at Cerro La Esmeralda was quite different from the conclusion that vegetation under plantation was similar to that of grazed páramo grasslands in a regional comparative study in Ecuador (Hofstede et al., 2002). The study in Ecuador applied one overall cluster analyse, including all páramo and plantation areas, to compare plant species diversity in plantation and natural páramo. It may well be that the regional patterns in plant diversity in Ecuador effectively masked pair-wise differences between plantation and páramo area. Additionally, in Ecuador the studied páramo sites included grazed páramo sites whereas evidence for grazing at the subpáramo site at Cerro de Esmaralda was lacking.

Many of the genera (e.g. *Ageratina*, *Baccharis*, *Bejaria*, *Brachyotum*, *Bucquetia*, *Cavendishia*, *Hesperomeles*, *Macleania*, *Miconia*, and *Monnina*) and species (e.g. *Arcytophyllum nitidum*, *Chaetolepis microphylla*, *Espeletiopsis corymbosa*, *Gaylussacia buxifolia*, *Lourteigia microphylla*, *Paepalanthus* aff. *columbiensis*, and *Stenorrhynchos vaginatum*) are often found in páramo and subpáramo belts in Eastern Cordillera of the Colombian Andes (Cleef, 1981; Van der Hammen and Cleef, 1986). In this respect the studied subpáramo vegetation is representative for the drier type of subpáramo found elsewhere in this cordillera. However, effects of pine tree afforestation may vary according to mesoclimate, edaphic conditions, age of plantation, and plantation management (Bockheim and Leide, 1991; Dames et al., 1998; Lips and Hofstede, 1998; Scholes and Nowicki, 1998; Hofstede et al., 2002). Caution remains needed when the results from this case study are to be extrapolated to other areas.

In conclusion, afforestation with *Pinus patula* resulted in strong negative effects on diversity and composition of the subpáramo vegetation at La Esmaralda. The higher the pine cover in the plantation plots, the stronger the reduction in plant species diversity and the higher the loss of typical, habitat-specific subpáramo species. When pine trees were found with low aboveground cover, their impact on plant species compositional patterns could not be separated from that related to habitat differences between plantation and subpáramo.

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