VEGETATION, CLIMATE, AND SOIL OF THE UNIQUE *PURDIAEA* FOREST OF SOUTHERN ECUADOR

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Abstract. Purdiaea nutans (Clethraceae) is a small evergreen tree scattered in montane forests of northern South America. In all known localities the species usually occurs sparingly, except in the Reserva Biológica San Francisco (RBSF) in southern Ecuador, where *P. nutans* is the dominating tree at elevations of between 2150 m and 2650 m. The abundance of large-stemmed, over 300-year-old individuals of *P. nutans* in the RBSF indicates that it is an old-growth forest. We explore the reasons for the occurrence of this unique forest type by comparing vegetation structure, climate, and soil of the *Purdiaea* forest with other upper montane forests in the region. We conclude that the exceptionally abundant occurrence of the species at RBSF is due to a combination of topographic, geological, pedological, climatic, and historical factors. The very broad upper montane ridges in the RBSF, very poor soils derived from the nutrient-deficient geological substrate, very high precipitation, and historical disturbances, including major past fires, have apparently permitted the development of the large stands of shrubby vegetation dominated by *P. nutans*. Accepted 20 December 2007.

Key words: Ecuador, *fire succession, montane forest, nutrient-poor tropical soils*, Purdiaea nutans, *ridge-top vegetation, tropical montane climate.*

INTRODUCTION

Purdiaea nutans Planch. (Clethraceae; see Anderberg & Zhang 2002) is a small evergreen tree scattered in montane forests in northern South America (Appendix 1, electronic supplement on the Ecotropica website). Characteristic are the narrow twisted stems, small xeromorphic leaves, slow growth, and occurrence on nutrient-poor soils (Huber 1995, Foster *et al.* 2001, 2002; Pennington *et al.* 2004, Homeier 2005). In all known localities the species usually occurs sparingly and with a few individuals only (e.g., Huber 1995, Foster *et al.* 2001, 2002; D. Neill pers. comm.), but in the Reserva Biológica San Francisco (RBSF), southern Ecuador, *P. nutans* is the dominant tree at elevations of between 2150 m and 2650 m (Bussmann 2001, Homeier *et al.* 2008). The forest dominated by *P. nutans* is a low-statured, shrubby, open woodland with trunks not higher than 5–10

(–15) m (Fig. 1). Accompanying woody species include members of Aquifoliaceae, Clusiaceae, Myrsinaceae, Myricaceae, Melastomataceae, Winteraceae, etc. The *Purdiaea* forest is physiognomically very different from upper montane forests elsewhere in Ecuador, which are characterized by a much higher (25–30 m) and rather closed canopy of *Weinmannia* spp. (Cunoniaceae), Lauraceae, Melastomataceae, etc. (Madsen & Øllgaard 1994, Jørgensen & León-Yánez 1999). The forest, moreover, is unusually rich in cryptogamic plants (Mandl *et al.* 2008).

Paulsch (2002) and Homeier (2004) noted that *Purdiaea* forest is mainly restricted to ridge habitats, and Schrumpf *et al.* (2001) described the soils of the *Purdiaea* forest as highly acidic, hygromorphic humaquepts. Hetsch & Hoheisel (1976), Grubb (1977), and Tanner *et al.* (1998) showed that low-statured, shrubby vegetations may develop in tropical high mountains on peaty, nutrient-poor soils. Our working hypothesis therefore was that the abundance of *P. nutans* was due to soil conditions.

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Interestingly, the species does occur at lower elevations in the RBSF, at 1800–2150 m, in forest with a high canopy to 20 m (Knörr 2003, Homeier 2004). In this habitat, however, *P. nutans* remains vegetative and does not rejuvenate. In a recent palynological study on the vegetation history of the RBSF, Niemann & Behling (2008) dated the mass occurrence of *Purdiaea nutans* in the RBSF at *ca.* 850 years B.P. and postulated a post-fire expansion of the species.

In an effort to understand the reasons for the development of this unique forest type, we have studied vegetation structure, climate, and soil of the *Purdiaea* forest and of other upper montane forests in southern Ecuador at similar elevations.

METHODS

Study sites. We studied montane ridge and slope forests between 2430 and 2650 m in three different localities in southern Ecuador: Reserva Biológica San Francisco (RBSF) and mountain pass El Tiro in the Río San Francisco area, and Cerro Tapichalaca Reserve further to the South (Fig. 2). The three sites were chosen to represent accessible, humid upper montane ridge forest at a similar elevation. The distance between RBSF and El Tiro is about 15 km, between RBSF and Tapichalaca *ca.* 90 km. We specifically searched for other sites with *Purdiaea nutans* in the study area but were unable to find any.

The RBSF (3°59'S, 79°04'W) is situated on the southern slope of the San Francisco river valley N of the Cordillera El Consuelo, a prominent side crest of the Cordillera Real separating the San Francisco and the Sabanilla valleys leading towards the Amazonian lowland. Ranging between 1800 m and 3140 m, RBSF preserves about one thousand hectares of humid evergreen mountain rain forests and páramo vegetation (Beck & Müller-Hohenstein 2001, Beck *et al.* 2008). The high relief energy, with steep and unstable slopes causing frequent occurrences of landslides, is a characteristic feature of the reserve. Geologically the area is made up of Paleozoic rocks consisting of meta-siltstones, sandstones, and phyllites with some quartz veins, dated as being of Devonian-Permian age (Litherland *et al.* 1994). Consequently, soils are poor in nutrients (Wilcke *et al.* 2001). Towards higher elevations soils become less well developed, accumulation of organic material increases, and hygrophytic soil properties become prominent (Schrumpf *et al.* 2001). Bussmann (2001) recognized four elevational vegetation belts: lower montane forest at 1800–2150 m (in ravines up to 2300 m); shrubby upper montane forest at 2150–2650 m; subpáramo dwarf forest at 2650–3050 m; and treeless páramo vegetation in the summit area at 3050–3150 m.

The mountain pass El Tiro (3°59'S, 79°08'W) is situated at *ca.* 2800 m along the Loja-Zamora road, 15 km W of the RBSF and on the border of Loja and Zamora-Chinchipe provinces, on the crest of the cordillera. The pass separates the dry interandean Río Zamora valley from the humid Río San Francisco Valley leading towards the Amazonian lowland. Our study site was located below the pass towards the east, in an area of very rugged topography with many small ravines and ridges overgrown by low-statured, shrubby cloud forest. Rocks at El Tiro belong to the same geological formation as in RBSF, being made up of meta-siltstones, sandstones, and phyllites with some quartz veins. Consequently, soils are very poor.

Cerro Tapichalaca Reserve (4°29'S, 79°07'W) is situated at ca. 2000–3400 m along the Loja-Zumba road in the Cordillera Real, *ca.* 90 km S of the town of Loja and just S of Podocarpus National Park. The area separates the dry interandean Río Solano valley from the wet Río Mayo valley oriented towards the Amazonian lowland and is made up of very wet montane cloud forest and páramo. Geologically, the Tapichalaca Reserve is made up of Mesozoic orthogneisses of the late Triassic (Litherland *et al.* 1994).

Vegetation. The extent of the *Purdiaea* forest in the Río San Francisco valley was visually mapped during August–November 2004, when *P. nutans* was easily identifiable from a distance by the prominent reddish coloration of young shoots and leaves (Fig. 1). Vegetation analysis was carried out in twenty-eight 400-m² randomly placed plots in ridge (12 plots) and slope locations (16 plots) at the three study sites. Vegetation parameters analyzed included tree species composition, abundance of *P. nutans*, estimated canopy height, estimated canopy closure, stem density, and basal area. Abundance of *P. nutans* was measured by estimating the ratio of individuals to the total of tree individuals. Nomenclature of tree species follows Jørgensen & Léon-Yánez (1999).

Climate. In all three sites, air temperature and air humidity at 2 m above ground level, precipitation, wind direction, and wind speed were measured by means of automated weather stations (THIES CLIM) from Thies GmbH, Göttingen. Sensors included a Pt 100 temperature sensor, digital hygro-transmitter,
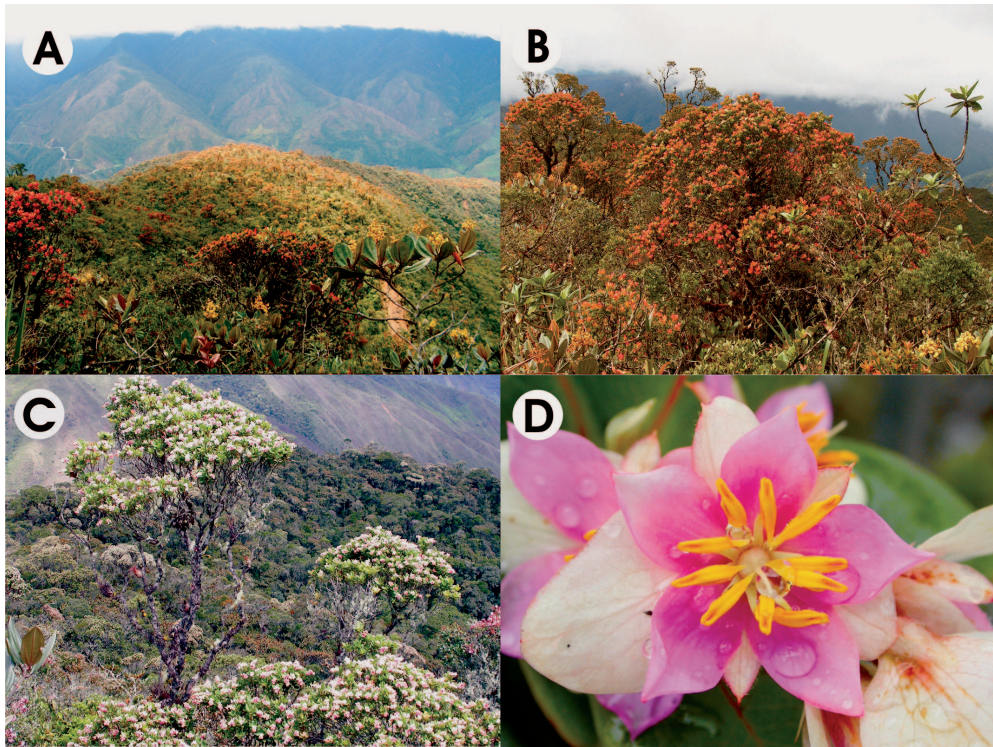
FIG. 1. The *Purdiaea* forest at the Reserva Biological San Francisco. A, B. Overviews showing characteristic red-colored foliage of *P. nutans*. C. Flowering individuals of *P. nutans*. D. Detail of flower of *P. nutans*; note characteristic asymmetrical, whitish calyx.

digital wind speed and wind direction transmitter, digital precipitation transmitter, and datalogger DL 15 (details: http://thiesclima.com). Evaporation was calculated by the Papadakis formula, which fits best with the Penman-Monteith equation (Schmiedecken 1979). Climate data at RBSF and El Tiro were recorded over four years (January 1999–March 2003), and at Tapichalaca over two years (September 2003–August 2005). The climate station at RBSF (TS1) was situated at 2670 m, at the upper end of the *Purdiaea* forest on a low ridge separating two small catchments on the NW-exposed slope of the cordillera, 20–200 m above the vegetation plots. The station has a leeward position within the windward escarpment of the deeply incised main range. The climate station at El Tiro was situated at 2840 m on the mountain pass, in a depression of the crest, *ca*. 250-400 m above the vegetation plots. The climate station at Tapichalaca was situated at 2510 m on a low ridge near Tapicha-

laca lodge, about 150 m below the crest, *ca*. 10-100 m below the vegetation plots.

Soil. In all vegetation plots soil profiles (organic layer, Ah and B horizons) in ridge and slope positions were sampled. Organic layer and mineral soil samples were carefully air-dried, sieved and ground for C and N analysis. Analyses were conducted for main physical (organic layer weight, texture, bulk density) and chemical (pH, exchangeable cations, organic carbon, total nitrogen, extractable P) soil parameters. Soils were classified according to the WRB-FAO-UNESCO-system.

Data analysis. Because of the close spatial proximity of the plots at a given study site, and the comparatively long distances between sites, study plots could not be used as independent data points in analyses covering more than one site. For this reason, we conducted a two-step analysis, first assessing the abundance of *Purdiaea* relative to study site and main

habitat (ridge, slope) via a two-way ANOVA. Secondly, for those site-habitat combinations with *Purdiaea* present, we conducted simple and multiple regression analyses between the abundance of *Purdiaea* and plot-specific parameters (elevation, soil data).

RESULTS

Vegetation. Visual mapping of *Purdiaea* stands in the Río San Francisco valley showed that the *Purdiaea* forest is restricted to ridge and upper slope habitats between 2150 m and 2650 m, on the southern side of the valley (Fig. 2). Large stands of up to 60 ha occurred where ridges are very wide and on exposed plateaus. Lower down the slopes, scattered mature and young individuals of *P. nutans* were recorded; the species was absent in ravines. The total surface area of *Purdiaea* forest was estimated at about 200 ha, more than half of it (115 ha) located in RBSF.

The higher abundance of *Purdiaea* on ridge habitats and at the RBSF site was confirmed by a two-way ANOVA, with significant differences between sites ($F_{3,25} = 75.61$, $P < 0.001$), habitats ($F_{2,26} = 83.22$, $P < 0.001$), and for the interaction between the two factors ($F_{6,22} = 64.79$, $P < 0.001$).

In all three localities canopy height, canopy closure, stem density and basal area were higher in slope forest than in ridge forest (Table 1). The ridge forest canopy was highest at RBSF and lowest at Tapichalaca; that of slopes forest, however, was similarly high at Tapichalaca and RBSF and lowest at El Tiro. Canopy closure varied considerably in ridge forests (Table 1); mean values were highest in Tapichalaca and lowest in El Tiro. On slopes, canopy closure was uniformly very dense (88–89%) in all three study sites.

Ridge forest of the RBSF was dominated by *Purdiaea nutans* (abundance averaging 80–100%; Table 1); frequent accompanying species were *Ilex rimbachii*, *I. scopulorum* and *I. weberlingii* (Aquifoliaceae), *Weinmannia elliptica*, *W. fagaroides* and *W. loxensis* (Cunoniaceae), *Clusia* spp. (Clusiaceae), *Cybianthus marginatus* (Myrsinaceae), *Calyptranthes pulchella* (Myrtaceae), and *Myrcia* sp. (Myrt.). In slope forest *P. nutans* was also dominant but much less so than on ridges (abundance averaging 20–40%). Frequent accompanying tree species were *Hedyosmum* spp. (Chloranthaceae), *Clusia* spp., *Licaria subsessilis* (Lauraceae), *Meriania rigida* (Melastomataceae), *Miconia* spp. (Melast.), *Podocarpus oleifolius* (Podocarpaceae), *Dioicodendron dioicum* (Rubiaceae), and *Drimys granadensis* (Winteraceae).

In ridge and slope forests of El Tiro *Purdiaea* was very scarce (abundance < 5%). Principal tree species on ridges were *Ilex rimbachii*, *Schefflera* spp. (Araliaceae), *Clusia* spp., *Weinmannia elliptica*, *W. fagaroides*, *Miconia* spp., *Calyptranthes pulchella*, *Siphoneugena* sp. (Myrt.), and *Ternstroemia jelskii* (Theaceae). On slopes *Ilex hippocrateoides*, *Clusia* spp., *Miconia* spp., *Calyptranthes pulchella*, *Podocarpus oleifolius*, and *Elaeagia ecuadorensis* (Rub.) were the most important woody taxa.

Ridge and slope forests in Tapichalaca resembled those of El Tiro but were conspicuous by the total absence of *Purdiaea* and the frequent presence of palms (*Geonoma* spp., *Ceroxylon parvifrons*). Common tree species in ridge forest in Tapichalaca, additional to palms, were *Ilex gabinetensis*, *Hedyosmum translucidum*, *Weinmannia fagaroides*, *Miconia* spp., *Myrica pubescens* (Myricaceae), and *Myrsine coriacea*; in slope forest *Hedyosmum* sp., *Clusia ducu*, *C.* sp., *Weinmannia fagaroides*, *Miconia* spp., *Myrsine coriacea*, *Myrcia fallax*, *Podocarpus oleifolius*, and *Drimys granadensis*.

TABLE 1. Forest structure (trees > 10 cm dbh) in the study plots. Canopy height, canopy closure, and *Purdiaea* abundance (= ratio of individuals to total tree individuals) are estimated values.

|	RBSF		El Tiro		Tapichalaca	
Location	ridge	slope	ridge	slope	ridge	slope
Number of plots	6	4	3	6	3	6
Elevation (m)	2450-2650	2500-2550	2550-2600	2430-2575	2550-2630	2520-2600
Purdiaea abundance (%)	(40-)80-100	(5-)20-40(-60)	<5	<5	—	—
Canopy height (m)	4-15	8-20	2-10	5-12	3-10	10-20
Mean canopy closure (%)	54±6	88±2	41±13	89±1	74±15	88±1
Mean stem density (400 m^{-2})	12.0±0.61	16.3±6.05	6.7±4.2	15.2±1.8	9.0±4.6	24.2±3.7
Mean basal area (m^2/400 m^{-2})	0.28±0.06	0.37±0.29	0.10±0.14	0.35±0.11	0.18±0.24	0.84±0.21
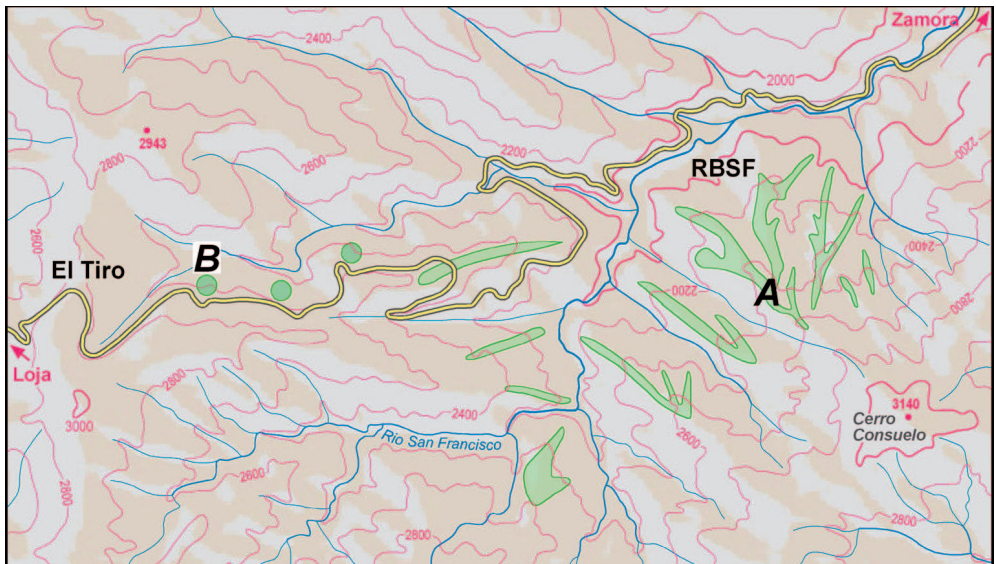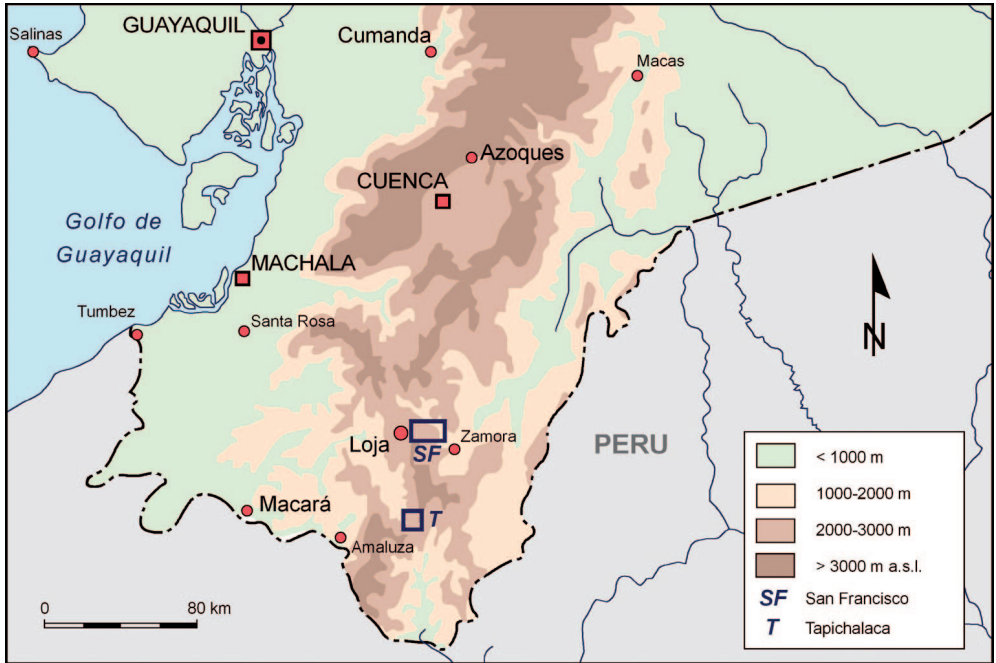
FIG. 2. Top: position of the study area (marked in blue) in southern Ecuador; SF: Río San Francisco valley; T: Cerro Tapichalaca reserve. Bottom: occurrence of *Purdiaea nutans* (in green) in the Río San Francisco valley; A (green elongated areas): *Purdiaea-dominated* forest; B (green dots): additional, non-dominating occurrence of *P. nutans*; RBSF: Reserva Biológica San Francisco.
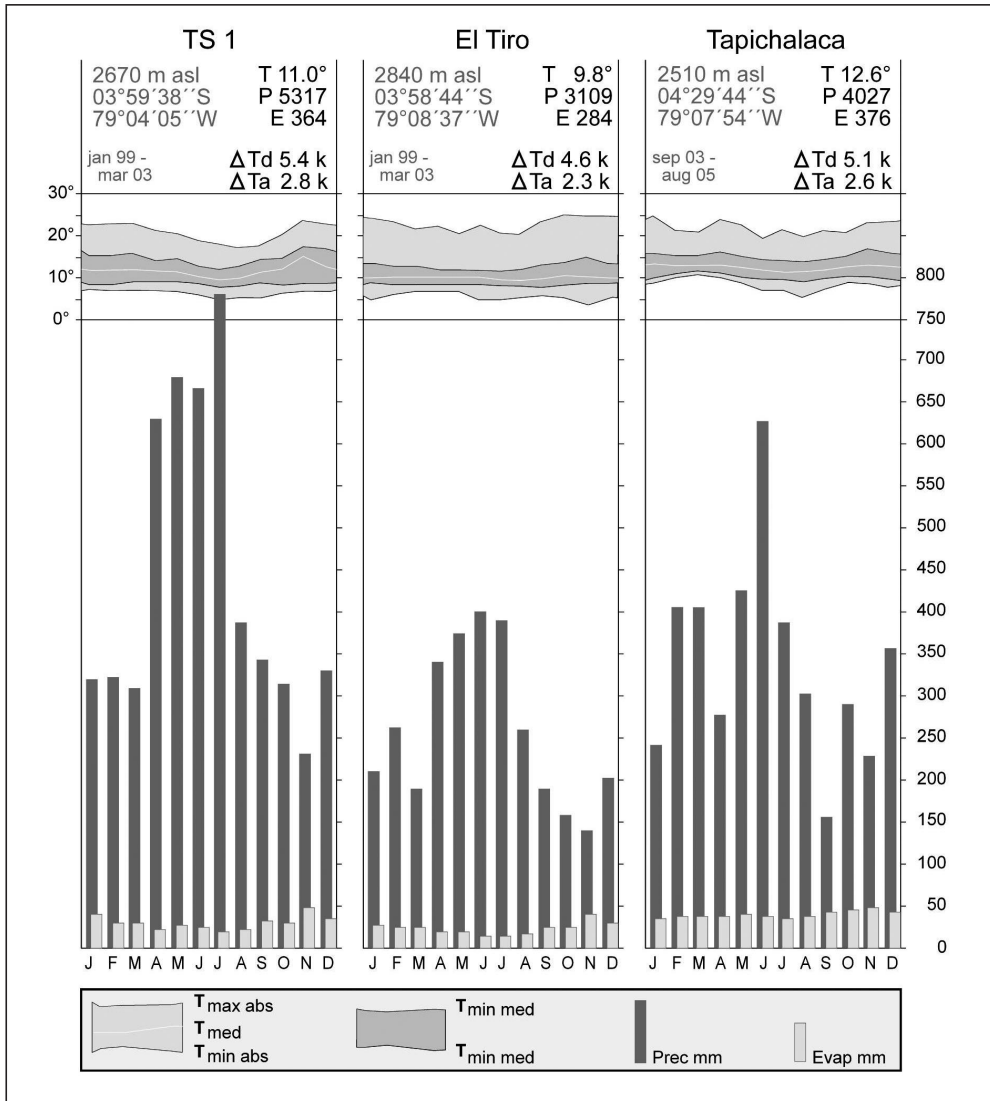
FIG. 3. Climate diagrams from the three study sites. For explanation see text. TS1 = climate station at 2670 m in the RBSF.

Graffenrieda harlingii (Melast.) was common in ridge and slope forests at all three study sites.

Climate. The climate at all three sites (Fig. 3) is permanently cool and perhumid, during 12 months annually (Richter 2003). Even during the 1998 El Niño event, climatic conditions at RBSF and El Tiro did not differ significantly from those during normal years (M. Richter, pers. obs.). Annual precipitation was high at all three sites, ranging from *ca.* 3000 mm at El Tiro to *ca.* 4000 mm at Tapichalaca and over 5000 mm at RBSF. Air humidity conditions outside the forest were almost similarly high at all sites, with relative annual mean values of 89 % at RBSF, 92 % at Tapichalaca, and 95 % at El Tiro. These values seemed to correlate with fog frequency, which was

highest at the crest line in El Tiro (J. Bendix, pers. comm.).

In accordance with elevation, air temperature means were highest at Tapichalaca (12.6°C) and lowest at El Tiro (9.8°C). Frost events were not recorded at any of the three sites. Temperature maxima occasionally rose up to 25°C and air humidity dropped to 25 % at all three locations in the period mid October–mid December, when monsoon-induced northwestern airstreams interrupt the semi-permanent easterly air flow. These are the only episodes with sunny weather and usually last only a few days.

Soil. Soils at all three study sites are acidic dystric cambisols and gleysols; no systematic differences between soil types were detected at the three sites. Organic layers are made up of mor-like wet humus with a thin Oi followed by thick Oe and Oa horizons. The boundary with the mineral soil is very sharp and translocation of organic matter into the mineral topsoil is mainly due to percolation of dissolved organic matter. Bioturbation by soil dwellers is almost absent.

Organic carbon contents in the organic layer were similar at all sites but nitrogen content slightly increased from El Tiro to Tapichalaca; Nt was higher on slopes than on ridges at all sites (Fig. 4). C/N ratios were highest at El Tiro and lowest (*ca.* 20–24) at Tapichalaca, indicating a more active matter turnover and mineralization activity at the latter site.

Organic carbon content in the Ah horizons varied between 2 and 5 %, with clearly higher values on slopes than on ridges (Fig. 5). Total N in the Ah horizon showed similar tendencies while Nt values in slope soil at Tapichalaca were highest. C/N ratios ranged between 15 and 30 with closer values on slopes (15.0–19.6) than on ridges (20.6–29.9). For available P no differences were detected between the sites but slightly higher values prevailed on slopes. In the B horizon highest Corg and N values occurred at Tapichalaca (slope), the other two sites did not differ, neither for Corg and N nor for available P.

As expected, soil reactions (H_2O) were very low in all mineral soil horizons and sites, given the acidic parent material; no systematic differences in pH values were detected between sites and between ridges and slopes. With the exception of RBSF, slope soils at the study sites contained more exchangeable K, Ca, and Mg compared with ridges. Highest values of K, Ca, and Mg were measured at Tapichalaca. Base saturation in Ah horizons was also higher in Tapichalaca slopes (16.4–17.8) compared with the two other sites (5.6–16.9). However, base cation contents were generally very low at all sites.

Within site-habitat combinations with *Purdiaea*, no significant relationships were found between the abundance of *Purdiaea* and any of the soil parameters or elevation (data not shown).
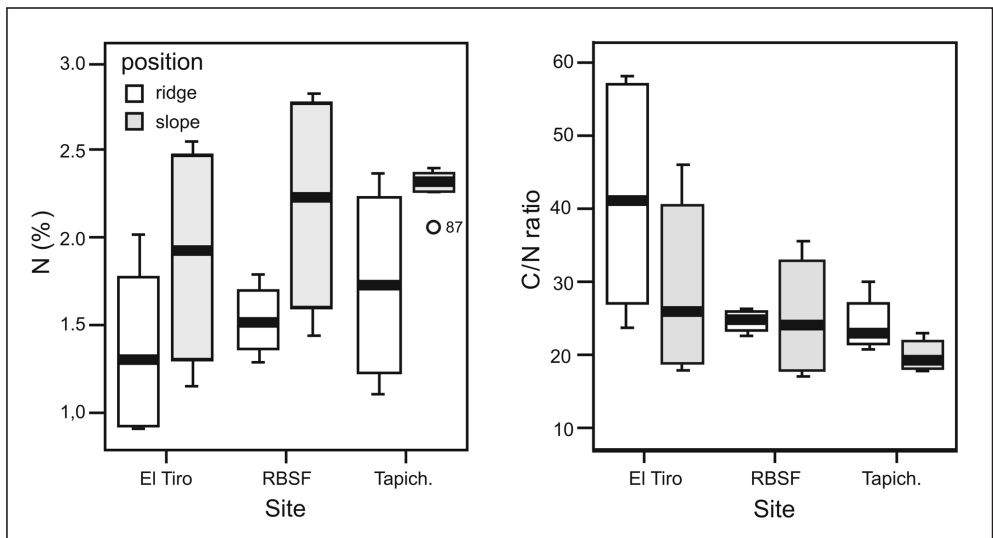

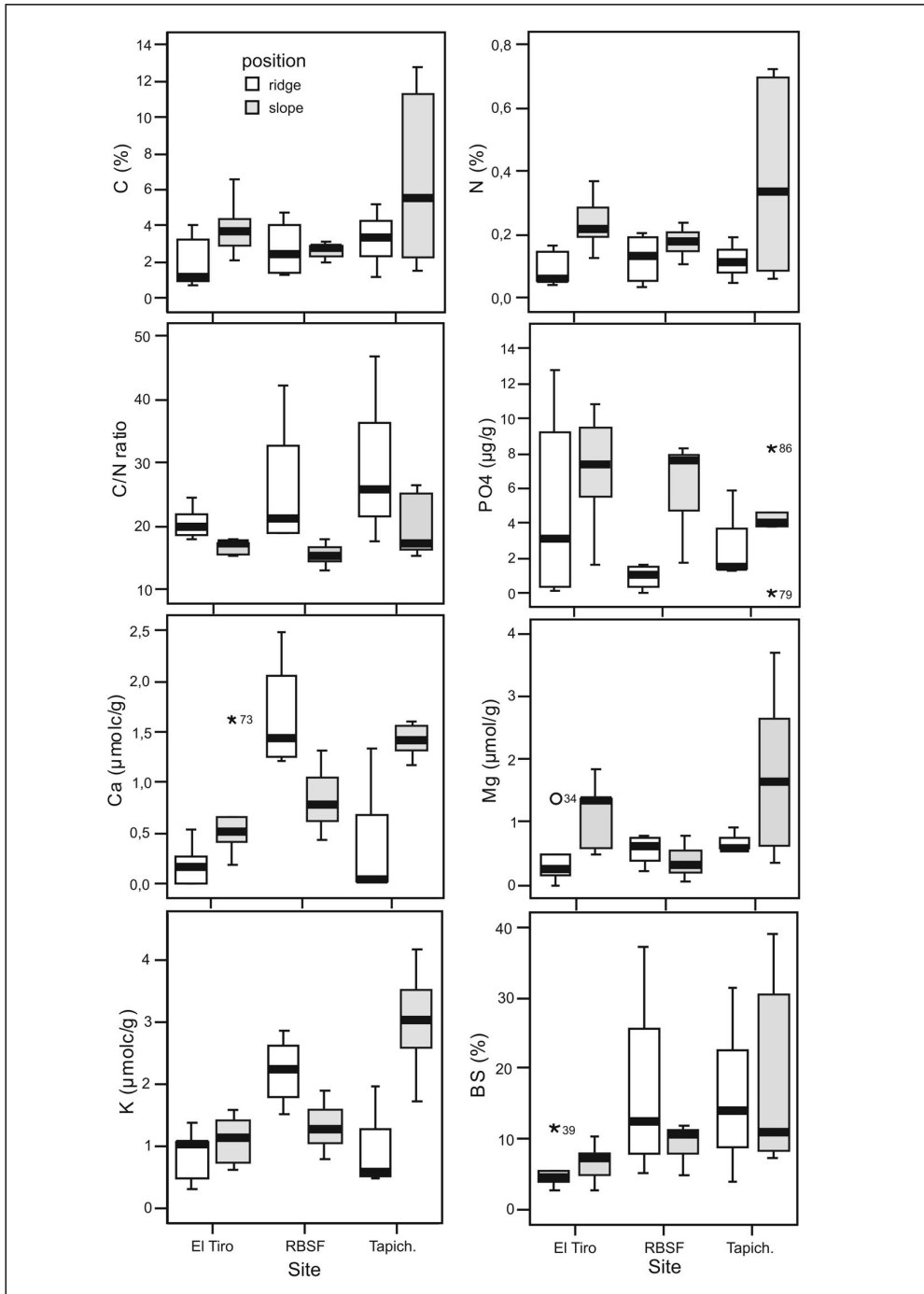FIG. 4. Total nitrogen (N) content and C/N ratio in the organic layer.

FIG. 5. Soil chemical parameters in the Ah horizons [org. Carbon (C), total nitrogen (N), C/N ratio, citric acid extractable PO_4^{3-} (PO4), exchangeable base cations (K, Ca, Mg) and base saturation (BS)].

DISCUSSION

Differences in tree community composition and forest structure in natural tropical forests are usually explained relative to climate (temperatures, precipitation), soil fertility (e.g., Tuomisto *et al.* 1995, Phillips *et al.* 2003, Paoli *et al.* 2006), and dispersal processes (e.g., Tuomisto *et al.* 2003). Most studies have been carried out in lowland areas; very few deal with mountain forest (e.g., Tanner 1977, Aiba & Kitayama 1999, Proctor *et al.* 1999). In the present study, we explored the causes of the development of the unique upper montane *Purdiaea* forest of southern Ecuador from three different abiotic points of view: soils (geology), climate, and topography.

Our study confirms that *Purdiaea nutans* is a ridge-top tree, as suggested previously by Foster *et al.* (2001, 2002) and Homeier (2004). Günter *et al.* (2008) have shown that *P. nutans* occurs abundantly in ca. 40-year-old secondary ridge forest at the RBSF but not in successional stages of the taller forest on nutrient-richer soils lower down the slopes. Knörr (2003) recorded seedlings and very young plants of *Purdiaea*, with stem diameters of less than 2 cm dbh, in mature, *ca*. 20-m-high slope forest, but not adult plants. Our observation is that adult individuals of *P. nutans* also occur in the tall slope forest but are very scarce. Thus it appears that the species is perfectly capable of regeneration on ridges in the RSBF. In the tall slope forests on nutrient-richer soils, however, growth conditions are apparently unfavorable for *P. nutans*; as a result the species is presumably outcompeted here by faster growing tree species (Homeier 2005).

Within the ridge habitat, we found a marked difference in the abundance of *Purdiaea* between our three study sites but were unable to find any relationships between *Purdiaea* abundance and plot parameters (soil, elevation) within sites. Accordingly, our interpretation of the causes of the dominance of *Purdiaea* at the RBSF is limited to a comparison between the three study sites. Since the rarity of *Purdiaea* restricted our study to these sites, we lack replicate study sites and are forced to base our conclusions on a qualitative comparison of the various parameters that differ to some degree between the three study areas. These include differences in soil nutrient conditions, precipitation, topography, and disturbance history.

Purdiaea nutans flourishes only on the poorest soils, where most other tree species vanish. However, our working hypothesis that the abundance of *P. nutans* was due to soil conditions was only partly confirmed. Soils on ridges were indeed more acidic and poorer in nutrients than those on adjacent slopes, but the differences in soil chemical properties among ridges with much, little, and no *Purdiaea* were minor. Only slightly higher base characteristics and indicators for higher C, N, and P turnover were measured at Tapichalaca, where *Purdiaea* is lacking, while Ca and K were more abundant at the RBSF where *Purdiaea* dominated. The development of poorer soils at the RBSF and El Tiro is caused by geological substrates consisting of nutrient-poor meta-siltstones, sandstones, phyllites and quartz, and the very high precipitation (over 5000 mm annually). In comparison, rocks at Tapichalaca are largely made up of ortho-gneisses (Litherland *et al.* 1994), which upon erosion produce soils richer in clay elements and therefore slightly richer in minerals. In addition to soil chemistry, water availability may also determine forest structure. Proctor *et al.* (1999) found that maximum tree height was directly proportional to the water retention capacity of soils in coastal tropical mountain vegetation of the western Philippines at 200–800 m elevation, but could not demonstrate a correlation between forest structure and soil chemical condition. However, due to the permanently cool and perhumid climate at the RBSF study site, with very high precipitation over twelve months, soil water supply in the *Purdiaea* forest is considered optimal during the whole year (Roederstein *et al.* 2005). Therefore we assume that soil chemical status rather than soil water retention is a major factor determining forest structure at our study site.

Neither does the development of the *Purdiaea* forest seem to be determined primarily by climatic factors. Annual precipitation was highest at RBSF, but El Tiro and Tapichalaca also had high values. However, even our "driest" site had about 3000 mm mean annual precipitation, which at elevations of about 2500 m and correspondingly low temperatures results in a perhumid climate. Therefore, it is unlikely that the precipitation differences between the sites result in physiologically relevant differences in water availability. More importantly, other records of *Purdiaea nutans* are from sites at lower elevations and hence higher temperatures, as well as from regions with abundant, but lower precipitation, showing that the species is not restricted to the wettest habitats.

Topographic features also showed some differences between the sites. At RBSF, the very wide extension of the ridges may have allowed the development of the large stands of shrubby vegetation dominated by *P. nutans*. The sparse occurrences of *P. nutans* at El Tiro, where ridges are very narrow, may thus be due to the different topography at this site.

Alternative explanations for the dominance of *Purdiaea nutans* at the RBSF site arise from recent work on population dynamics and regeneration of the species, and from palynological data. Recent palynological work in the RBSF (Niemann & Behling, 2008), suggests that past fire events may have played an important role in the establishment of *Purdiaea nutans*. Charcoal remains at this study site have been dated at *ca*. 850 years B.P. Prior to this fire event, genera that are typical of slope forests, such as *Ilex* and *Podocarpus*, were more common than at present while *Purdiaea* was rare, indicating a wider distribution in the area of typical tall montane forests. Records of maize (*Zea*) pollen following the main fire events suggest that human agricultural activity occurred in the area. Thus, past fires seem to have markedly influenced the floristic composition of the forests at the RBSF (Niemann & Behling, 2008). The palynological data suggest that the expansion of *P. nutans* in the RBSF occurred after the reduction or absence of fires in combination with a decline of human activities in the area *ca*. 850 years ago.

Purdiaea nutans is highly resistant to fire (M. Lehnert & N. Mandl, pers. obs.). It is therefore conceivable that *Purdiaea* may have survived fire events better than other trees and may have taken advantage of the resulting open post-fire vegetation structure to achieve extensive regeneration. Growth measurements have shown an average annual increase in stem diameter of *P. nutans* of *ca*. 0.6 mm (Homeier 2004, 2005). Based on these data, the age of mature *Purdiaea* trees in the study area is estimated to be at least 300 years. The very slow growth of the species may have slowed succession processes to such a degree that even after 850 years the dominance of *P. nutans* in ridge habitats is still unbroken. The open structure of the *Purdiaea* forest, allowing the development of a dense terrestrial herbaceous vegetation cover dominated by bromeliads (Bussmann 2001), may also limit the establishment of tree seedlings in *Purdiaea*-dominated ridge forests. In contrast, succession may have proceeded at a faster pace on the slopes with their more benign abiotic conditions, leaving only scattered old individuals of *Purdiaea* as relicts in a forest now dominated by faster-growing, taller trees. In this scenario, the dominance of *Purdiaea* at the RBSF might, in the absence of further disturbances, be expected to slowly decrease in the future.

In conclusion, we found that *Purdiaea nutans* is clearly a ridge-top species. Regarding the dominance of the species at the RBSF, we found slight differences in soil and climatic conditions between the three study sites but consider these unlikely to be the main factors determining the abundance of *Purdiaea*. Rather, the historical data may explain why *Purdiaea nutans*, a tree species that is abundant on ridges in the RBSF but that is normally rare, could have achieved atypical dominance at a single site. Additional support for this hypothesis may be obtained through more detailed paleo-ecological data and experimental work, e.g., through transplantation of typical slope forest trees such as *Ilex* or *Podocarpus* into *Purdiaea*-dominated stands where herbaceous ground vegetation has been removed. Unplanned "experiments" may involve fire events at non-protected sites where *P. nutans* is currently scarce, allowing for study of post-fire regeneration of the species.

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Additional material to this paper is available at
    http://www.gtoe.de/?page_id=75

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