

THE BRACKEN FERN (*PTERIDIUM ARACHNOIDEUM* (KAULF.) MAXON) DILEMMA IN THE ANDES OF SOUTHERN ECUADOR

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Abstract. Bracken fern (*Pteridium aquilinum* (L.) Kuhn) is one of the world's most powerful weeds, especially in agricultural areas. Its vigor and resistance to any kind of non-polluting pest control result from its extensive rhizome system. Growth of this rhizome system is strongly promoted by fire. As elsewhere in the tropics, farmers in the Andes of southern Ecuador make extensive use of fire to convert primary forest into arable land and to maintain their pastures. This communication addresses, from a phytosociological viewpoint, the ecological problems arising from the use of fire as an agricultural tool in the presence of the extremely aggressive and fire-tolerant bracken fern *Pteridium arachnoideum*. Repeated burning of the pastureland weakens the competitive strength of the most important pasture grass *Setaria sphacelata*, while the competitive strength of bracken increases. Pastures are finally abandoned when *Pteridium* has become completely predominant. Wind-dispersed seeds of several weedy Asteraceae and Melastomataceae species germinate under the canopy of the bracken leaves and, due to the steepness of the slopes, the seedlings receive sufficient light for further growth. The majority of these species are bushes that finally overtop the bracken leaves and can successfully compete with the shade intolerant fern. A vegetation composed of dense patches of *Pteridium* interspersed with individual bushes develops, which, because of the immense seed production of the bushes and the vigor of the bracken, is very stable and appears to be a long-lasting and even at times the final successional stage. Since natural regeneration of the indigenous forest is very unlikely in these areas, reforestation may be the only way out of the dilemma caused by the extensive use of fire and the fire-tolerance of bracken. Accepted 28 January 2003.

Key words: Bracken, *Pteridium arachnoideum*, vegetation analysis, agricultural problems, southern Ecuador.

INTRODUCTION

Bracken (*Pteridium aquilinum* (L.) Kuhn, Dennstaedtiaceae) is considered to be one of the world's most powerful weeds (Webster & Steeves 1958, Page 1976). Everywhere from the tropics to the temperate zone it renders arable land that has been wrested from forests by the use of fire useless. The taxonomy of this fern is still a matter of investigation: molecular data are providing new insights into how the two major groups, the "aquilinum" group of the northern, and the "caudatum" group of the southern hemisphere, are related to one another and to the diversity occurring within each of the groups (Thomson 2000, Thomson & Alonso-Amelot 2002). Bracken is a typical representative of serial stages following the clearing of forests. Its competitive strength benefits considerably from any kind of forest clearing and in particular from the use of fire. The special virtue of its

differentiated rhizome system (Webster & Steeves 1958) for rapid colonization of new areas has been reported by many authors (e.g., Watt 1976, Page 1982). Especially the long shoots of the rhizome develop rapidly after warming of the soil by a fire, whereas the frond-bearing laterals, which branch out from them, grow comparatively slowly. The reason for these differential growth rates is not known. Due to its outstanding competitive strength, bracken hinders reforestation and the regeneration of the original ecosystems (Humphrey & Swaine 1997). In addition, it creates severe problems in pasturelands, due to the toxicity of its fronds (Petrov & Marrs 2001). Many measures have been implemented to control bracken in agricultural areas, but none has had sustainable success (Marrs *et al.* 2000). This failure is due to the vigor of the rhizome system of this fern, which forms a dense network at several depths of the soil. Therefore, at least part of the plant is effectively protected from fire, from damage by mechanical weeding (Lowday 1986, Fenwick 1989), and from most herbicides with the po-

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tential exception of "Asulam" (*N*-(4-Amino-benzoylsulfonyl)-carbamic acid-methylester). This herbicide is incorporated via leaves and transported to the roots, weakening the plant at least temporarily by inhibition of cell division (Williams & Fraser 1979). Bracken infestation of a cleared area is not only caused by the vegetative growth of the long rhizomes but can also result from sexual reproduction, since a single frond can annually produce up to 300000000 spores (Conway 1952, 1953, 1957), which germinate without any dormancy requirement and are viable for about 1.5 years (Page 1986). The very light spores are easily dispersed by wind and young plants can be observed 6–7 weeks after the spores have been shed, in particular if the soil has been sterilized by fire (Conway 1949, Mitchell 1973). The individual subspecies and varieties of *Pteridium* vary in aggressivity and size: the smaller subspecies of the northerly varieties are less aggressive than the taller ones of the southern races. After slash and burning in the northwestern United States, *Pteridium aquilinum* var. *latifolia* covered less than 1% of both the burned area and an unburned control area (Steen 1966), while shortly after a fire in tropical Ecuador, bracken (identified as *P. arachnoideum* (Kaulf.) Maxon) covered more than 25% of the burned area. Allelopathic effects have been attributed to compounds of bracken fronds, inhibiting the growth of the neighboring vegetation (Gliessman 1976). On the other hand, bracken leaves are hardly ever attacked by insect pests, a fact that may result from the toxicity of the fern and its protection by ants, which feed on the extrafloral nectaries of the plant (Tryon 1941, Lawton 1976). However, bracken appears to be specifically attacked by the fungus *Ascochyta pteridis* that readily infects and kills young leaves but is less virulent on mature leaves (Webb & Lindow 1987).

Due to the extraordinary vigor of its tropical varieties in particular, bracken is the most serious pest on all agricultural land that has been acquired and maintained by repeated burning. We report on the ecological problems created by the use of fire as an agricultural tool and the presence of bracken in the mountains of southern Ecuador on the basis of phytosociological data.

METHODS

Details of the study area in the Rio San Francisco valley between the provincial capitals Loja and Zamora have been presented by Beck & Müller-Hohen-

stein (2001). Briefly, the area is a deeply incised valley whose southern slopes are covered by a more or less dense primary and secondary rain forest. The forest has been cleared for farming purposes on the northern slopes, from the valley bottom almost up to the crest of the ridges. The present study is based on the areas of seven farms (so-called fincas), whose location is shown in Fig. 1. Land-use practices in these areas have been described in detail by Paulsch *et al.* (2001). Areas representing different serial stages of succession were selected to achieve a space-for-time substitution (Pickett & White 1986) for an assessment of vegetation dynamics. Relevé-based vegetation analysis was performed according to the method of Braun-Blanquet, as described by Mueller-Dombois & Ellenberg (1974), and modified by van der Hammen *et al.* (1989). Minimum areas were 4 m² on homogeneous pasture and 25 m² on abandoned agricultural land. Plants were identified using the Flora of Ecuador (Wurdack 1980, Soejarto 1982, Byge 1989, Gustafson 1992, Anderson 1993, Berg & Rosselli 1993, Pringel 1995, Luteyn 1996, Romoleroux 1996) and by comparison with specimens in the herbaria of the Estación Científica San Francisco and the Universidad Nacional de Loja, in which duplicate samples have been deposited. For analysis of the relevés the program SORT (Durka & Ackermann 1993) was used.

RESULTS AND DISCUSSION

Growth of Pteridium after clearing of the primary forest. Interviews with the local farmers confirmed our observations that burning is still the common method of clearing the primary forest in order to acquire new areas for agricultural purposes. Every fire, irrespective of being lit inside or at the edge of the forest, kills trees either by burning or because of the resulting heat. A fringe of dead, but not charred, trees is always found at the margin of a burnt area. After some time, when these heat-killed trees have completely dried up, the fringe can be used to start a new fire. The remnants of a previous burning – charred trunks and large branches – are frequently left where they have fallen on account of the enormous efforts which would be required to remove them from steep and remote areas. Therefore an area is burned repeatedly until the spaces between the remaining logs are wide enough to plant beans or maize or the pasture grasses *Setaria sphacelata* (Schumach.) Stapf & C.E. Hubb. ex Chipp., and *Melinis minutiflora* P. Beauv.



FIG. 1. Map of the San Francisco valley between Loja and Zamora in southern Ecuador. “ECSF” is the research station “Estacion Cientifica San Francisco”. The crest of the mountains is at about 2600 to 2700 m a.s.l in the north and at 3000 to 3100 m in the south. The red dots indicate the fincas, where relevés were recorded. Forested areas are shaded in green while cleared areas are indicated in white.

A few weeks after an initial fire *Pteridium arachnoideum* was observed sprouting vigorously on both the burnt and the heat-killed areas, while it was absent in the intact primary forest. The size and shape of the primary leaves (about 25 cm in total height) and the morphology of the fern's rhizomes indicated that this kind of *de novo* colonization was accomplished mainly by a rapid development of leaf-producing lateral branches of the quickly elongating main axes (Watt 1940, Daniels 1985), which had already entered the heat-killed fringe of the forest from the previous clearing. The colonizing rhizomatous long-shoots are usually buried deep in the soil (down to 0.7 m) and are thus well protected from fire.

Spreading into new areas by means of sexual propagation is less probable, in spite of the immense number of spores that may be produced by the fronds (Conway 1957, see above). Gametophytes of the fern were not found in recently cleared areas. Since the young sporophytes arising after a few weeks on the prothalli produce a single lobed frond (Conway 1949,

Conway 1957), such gametophytes would have been easily recognizable on the bare soil surface. The apparent insignificance of sexual propagation for the colonization of cleared areas differs from reports from Costa Rica, where gametophytes amply cover the bare or ash-covered soil after a fire (Gliessman 1978).

Competition between bracken and pasture grasses. Both bracken and crops develop simultaneously after burning. Depending on the vigor of *Pteridium* in their fields, the farmers sooner or later replace their crops with pasture grasses, in particular *Setaria sphacelata*, which tolerates burning. *Setaria* is planted manually in horizontal rows (Fig. 2), and the bracken fronds protrude mainly from the spaces between the tussocks. *Setaria* grows initially a little faster than bracken (Fig. 3), and these areas can therefore be grazed by the cattle. *Pteridium* may even improve the nutrient availability of the soil by means of its root exudates, (Waring & Major 1964, Mitchell 1973, Williams *et al.* 1987) and thus initially enhance the growth of



FIG. 2. A new *Setaria sphacelata* plantation on a recently cleared area of primary forest. Heat-killed trees and some charred trunks and branches are witness to the mode of clearing by fire. Even at this very early stage of a plantation bracken is already present, discernible by its horizontally orientated leaves (in the center of the photograph). Photo E. Beck, 2001.



FIG. 3. Competition between *Setaria sphacelata* and *Pteridium aquilinum* about 4 weeks after a fire set by farmers for pasture amelioration. The soil between the tussocks is still covered with charcoal. Note that only the tips of the grass tussocks have been browsed by the cattle. Photo E. Beck, 2000.

the grass. However, the fern soon overtops the grass tussocks, and by shading them weakens their competitive strength and also their accessibility for the cattle. Since only the very young leaf blades and the tips of the mature leaves of *Setaria* are eaten by the cattle (Fig. 3), the carrying capacity of these pastures is low. The same is true for the steep parts of the slopes, where *Setaria*, because of the shallow soil cover, is replaced by the stoloniferous, curtain-forming *Melinis minutiflora*. This grass maintains only one to three green leaves on a shoot and thus produces only a small amount of biomass. Bracken is not eaten by the cattle, which is in agreement with its well-known toxicity (Evans 1986, Hannam 1986, Petrov & Marrs 2001).

In many places, efforts by the farmers to weaken the competitive strength of bracken by cutting the fronds or just by trampling on them can be observed. Repeated cutting of the leaves appears to be the most effective method (Lowday 1986), but it is very labo-

rious and, due to the exodus of farmers, the available manpower is not sufficient for treating larger areas in this way. The farmers traditionally consider repeated burning of their *Setaria* pastures as the only solution to the bracken dilemma, but recurrent fires in fact aggravate the problem. The pastures are usually burned during the drier months of the year, i.e., October to December. A few days after a fire, bracken and *Setaria* resprout more or less simultaneously, and the grass again produces the desired new leaves a little faster than the fern develops its leaves. However, the period of better grass growth becomes shorter with every fire due to the increasing density of the fern rhizomes, combined with an ongoing weakening of the grass tussocks as a result of the combustion of a substantial proportion of their biomass. Whether allelopathic compounds liberated from the *Pteridium* litter (Gliessman & Müller 1972, Gliessman 1976) also contribute to the decrease in the competitive strength of *Setaria* is

TABLE 1. Phytosociological analysis of the successional development of two types of pastureland subjected to different intensities of regular burning. *Melinis* pastures: low frequency of fires, *Setaria* pastures: high frequency of fires.

Species / stages	<i>Melinis minutiflora</i> pastures										<i>Setaria sphaacelata</i> pastures														
	early stage			late stage			early stage				late stage			abandoned pastures: <i>Peperidium</i> bushland											
Number of relevés	5	21	25	23	22	17	7	1	34	15	18	30	19	20	13	27	3	6	14	16	9	26	4	29	
Altitude (m)	1990	1830	1750	1860	1850	1850	1990	2050	1950	1580	1890	2520	1700	1700	1980	1840	2050	1980	1980	1900	1970	2140	2100	2124	
Plant cover (%)	90	100	95	100	100	100	100	100	100	100	90	100	100	100	100	100	100	100	100	100	100	100	100	100	
Number of species	10	10	20	13	13	7	19	28	13	6	5	6	11	9	23	15	17	23	10	12	16	22	28	11	
<i>Peperidium aquilinum</i>	1	+	1	1	4	3	5	+	1	•	1	+	+	3	+	1	4	2	1	1	2	1	2	•	
<i>Rubus</i> sp.	•	•	1	1	1	1	1	+	1	•	•	•	+	1	2	1	•	1	1	1	1	1	•	•	
<i>Monochaetum lineatum</i>	1	•	+	1	1	•	1	+	+	•	+	•	1	•	•	•	+	•	•	•	+	•	•	1	
<i>Andropogon bicornis</i>	•	•	•	1	1	•	•	+	•	•	•	•	•	•	•	•	1	1	•	•	•	•	•	•	
<i>Manettia alba</i>	•	1	1	+	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Chevreulia acuminata</i>	1	+	•	•	•	•	•	1	+	•	•	•	•	•	•	•	+	•	•	•	•	•	•	•	
<i>Melinis minutiflora</i>	5	5	4	4	4	4	3	1	1	•	•	1	•	•	1	•	•	•	•	•	•	•	•	•	
<i>Tibouchina laxa</i>	•	•	1	+	•	•	4	3	1	•	•	•	•	•	+	1	•	•	•	•	•	1	•	•	
<i>Borreria laevis</i>	+	1	•	•	•	•	•	+	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Setaria sphaacelata</i>	•	•	1	•	•	•	•	•	4	4	4	4	5	1	3	1	•	1	•	•	•	•	•	•	
<i>Abyrium dombeyi</i>	•	•	1	•	•	•	•	•	•	•	•	+	•	3	•	•	•	•	•	•	•	•	•	•	
<i>Eupatorium procerum</i>	•	•	•	•	•	•	1	+	•	•	•	•	•	•	3	3	•	+	•	•	•	•	•	•	
<i>Baccharis gonistelloides</i>	•	•	+	•	•	2	•	•	•	•	•	•	•	•	•	•	2	1	•	•	•	•	•	•	
<i>Baccharis latifolia</i>	•	•	2	+	1	•	1	1	•	•	•	•	•	•	•	1	2	2	4	2	1	1	2	•	
<i>Ageratina dendroides</i>	•	•	•	1	?	•	•	•	•	•	•	•	•	•	•	•	+	2	2	2	3	1	•	2	
<i>Munnozia senecioides</i>	•	•	•	•	•	•	•	+	•	•	•	•	•	•	•	•	•	•	•	1	1	•	•	1	
<i>Chusquea uniflora</i>	•	•	•	•	•	5	•	•	•	•	•	•	•	1	+	•	1	5	1	5	1	+	2	1	
<i>Lycopodium</i> sp.	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	5	1	•	•	•	•	1	2	•
<i>Viburnum pichinchense</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Axonopus compressus</i>	•	+	1	2	•	•	•	1	•	•	3	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Smilax mollis</i>	•	•	•	•	•	•	•	•	•	•	1	•	•	•	•	•	•	1	•	•	•	•	•	+	
<i>Smilax benthamiana</i>	•	•	1	•	•	•	•	1	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1	1	

Further species without significant occurrence

Apium montanum, *Blechnum cordatum*, *Carex* sp., *Cerastium* sp., *Conyza canadensis*, *Desmodium campylocladus*, *Gadinsoga parviflora*, *Galium hypocarpium*, *Graffenrieda* sp.1, *Ichnanthus pallens*, *Kankea* sp., *Kyllinga pumila*, *Lagascea mollis*, *Linum polygaloides*, *Munnozia hastifolia*, *Pilea abietifolia*, *Piptocoma discolor*, *Solanum* sp. 2, *Solanum guineense*, *Sichers rubiginosus*, *Trifolium repens*, *Viola arguta*.

Achyrocline alata, *Ageratina* sp.1, *A. ecartovensis*, *Alchornea* sp., *Andropogon leucostachys*, *Anthurium* sp., *Apium montanum*, *Baccharis macrantha*, *Bejaria aestuans*, *Bidens* sp., *Blechnum cordatum*, *Brachyotum campanuläre*, *Cerastium* sp., *Ceratosolenia lanatifolium*, *Chusca* sp., *Cortaderia jubata*, *Cyathea straminea*, *Disigona microphyllum*, *Elaphoglossum* sp., *Elaphoglossum* sp.1, *Erato polymoroides*, *Eriocaulaceae*, *Galinsoga parviflora*, *Galium aparine*, *Gaultheria erecta*, *G. reticulata*, *Hedyotum anisodorum*, *Heliotropium* sp., *Hordeum muticum*, *Isachne rigens*, *Juglans neotropica*, *Liatrum igniarium*, *L. bougainvii*, *Linum polygaloides*, *Lycopodiella thrysoides*, *Macrocarpaea renolata*, *Mikania* spec., *Muehlenbeckia tamnifolia*, *Munnozia hastifolia*, *Myrsine* aff. *acutiloba*, *Nectandra laurei*, *Neprolepis sp.*, *Peltocorea* sp., *Pennisetum peruvianum*, *Philoglossa peruvianum*, *Pilea abietifolia*, *Poa pratensis*, *Psychotria* sp.1, *Saurauia aspera*, *Sobralia fimbriata*, *Sida rhombifolia*, *Sichers arachnoides*, *St. tomentosus*, *Tabebuia chrysanthia*, *Tibouchina leptidacea*, *Trifolium repens*, *Vernonia baccharoides*, *V. arguta*, *Viola* sp.1.

not known. Finally, after less than 10 years on average, bracken takes over completely and the pastures are abandoned.

Pastures in which bracken has hardly any chance of growth and survival are the so-called “*Pastos azules*” which are usually found in geomorphologic flattenings and troughs with compacted and waterlogged soils. Cattle stay there for a longer time and their dung gives rise to a vigorously growing nitrophilous grassland, which is never burned by the farmers. Both the type of soil and the absence of fire prevent colonization of these pastures by *Pteridium*. Likewise, *Melinis* grassland is rarely set on fire, because this grass apparently does not resprout from the roots and recovers only from seeds. But as a result of the high incidence of burning, farmers sometimes lose control of a fire and then *Melinis* grassland can also burn and subsequently be successfully invaded by bracken (Table 1).

Bracken-dominated vegetation is not the final stage of succession. Bracken may produce a closed canopy on flat areas, thus preventing the establishment of a shade-intolerant vegetation, but on the steep slopes of the deeply incised valleys of southern Ecuador the fern canopy is open due to the predominantly horizontal orientation of the fronds. Wind-dispersed seeds and light can penetrate the canopy and a considerable variety of herbaceous and shrubby plants are found in addition to *Pteridium* in abandoned pasturelands (Fig. 4). In particular, two species of Asteraceae: *Baccharis latifolia* and *Ageratina dendroides*, and two of Melastomataceae: *Monochaetum lineatum* and *Tibouchina laxa* can successfully compete with the shade-intolerant (Page 1986, Stuart 1988) fern. Especially the bushy Asteraceae survive the recurrent fires and resprout from the bases of dead branches at the same time as the new fern fronds emerge. The final result is patchy vegetation in which islets of bracken are



FIG. 4. The final successional stage of vegetation on former agricultural land. Up to 3 m-high bushes (e.g., *Baccharis latifolia*, right, and *Ageratina* sp., left) are interspersed in the bracken canopy. Some of the dead *Pteridium* leaves exhibit a whitish and shiny surface, indicating that they have been attacked and killed by a pathogenic fungus, tentatively identified as *Ascochyte pteridis*. The pasturegrass *Setaria sphacelata* has completely disappeared from these areas. Photo E. Beck, 2000.

separated by the 2–3 m-high bushes (Table 1). This is a highly stable type of vegetation (Fig. 5), due to the high propagation potential of the bushes from seeds and of the fern via rhizomes. It was encountered in many areas of former agricultural use and thus appears to be at least a long-lasting serial stage or even a climax. The described successional sequence of stages has been documented phytosociologically and is shown in Table 1.

Potential biological control of bracken by a pathogenic fungus. An effective method of controlling bracken growth in tropical agricultural areas has not yet been attained. In the long term, a probably pathogenic fungus could potentially weaken the vigor of the bracken. The mycelia of this fungus overgrow the young fronds, rendering them silvery and glossy in

appearance (Fig. 4). A pinnule of an infected leaf was placed on an agar medium and an almost uniform mycelium developed within the course of a few days. Later on, other microorganisms also germinated on the agar. Controls using non-infected pinnules showed only growth of ubiquitous microorganisms. Although the fungus has not yet been identified, the characters of the mycelium grown from the infected fronds were in close agreement with those reported for the Ascomycete *Ascochyta pteridis* (Bres.) Sacc. (Webb & Lindow 1987). An optical check of all fern species encountered in the San Francisco valley revealed that the fungus successfully attacked only bracken. Interestingly, infection showed a high patchiness that was unexpected considering the genetic uniformity of *Pteridium*, assumed to be due to the predominantly vegetative propagation of the fern. To what extent in-



FIG. 5. View of the northern (south-facing) slopes of the San Francisco valley with a small remnant of primary forest on the crest (arrow). The bright green areas are plantations of the pasture grass *Setaria sphacelata*, interspersed with small patches of *Melinis minutiflora* grassland on the steeper parts of the slopes. *Pteridium* bushland, discernible on the photograph by the grayish-green color, is the predominant vegetation on these slopes. Most of it represents former agricultural land, mainly pasture, which has been abandoned due to the prevalence of bracken and weedy bushes. Above the right-hand patch of *Setaria* grassland, and on its left side, recent invasion of bracken into the pasture is obvious from the mixture of the bright green and the grayish color. Photo E. Beck, 2002.

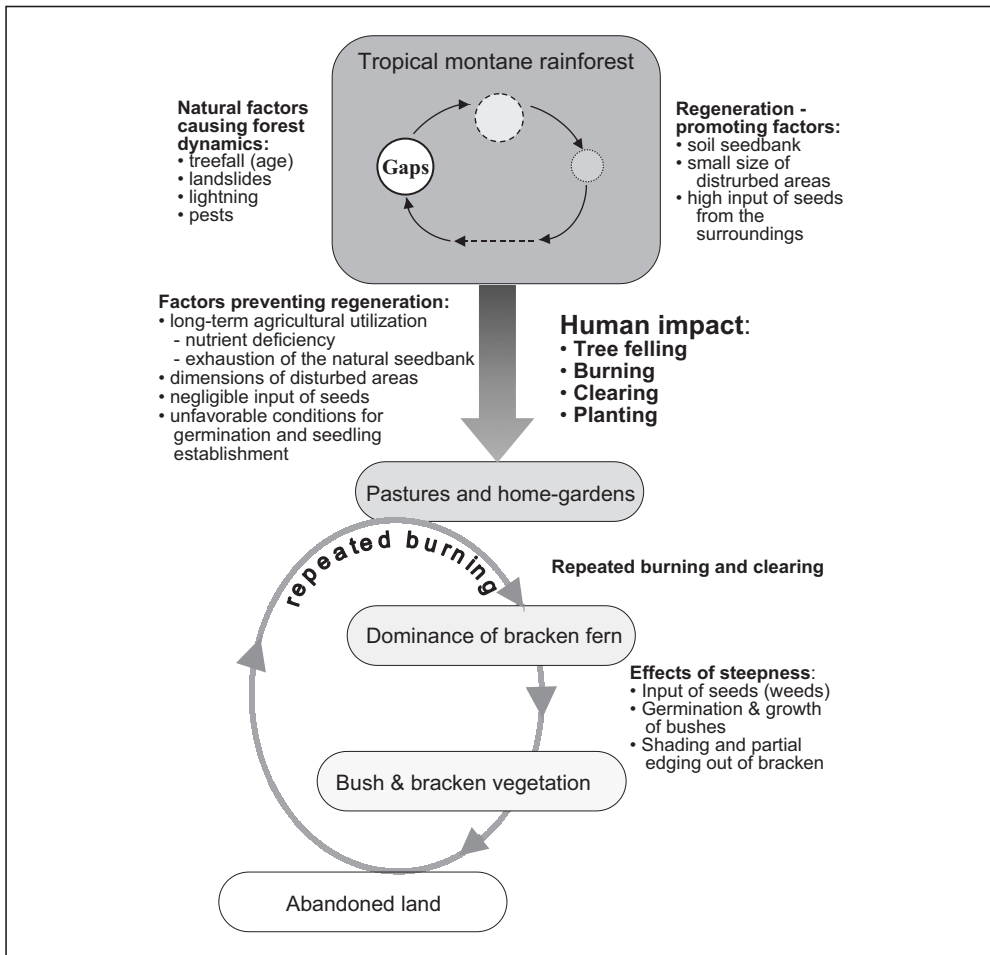


FIG. 6. Schematic representation of the ecological situation caused by human impact on the tropical mountain rainforest in the Andes of southern Ecuador. The use of fire and the ubiquitous presence of the bracken *Pteridium arachnoideum* are the main reasons for the naturally irreversible and detrimental development of agricultural land.

fection and killing of the leaves by the fungus impairs the viability and growth of the rhizomes has still to be investigated.

CONCLUSIONS

Ecological consequences and the question of forest regeneration on abandoned pastures. The rapid development of plant cover after a fire is favorable from an ecological viewpoint because it prevents soil erosion

by splash and the loss of mineral nutrients. In addition, landslides, which are very common in the pristine forests of that area, have never been observed in the weeded and abandoned former agricultural areas. This observation suggests that the weight of the vegetation cover is one of the crucial factors determining the stability of the usually water-soaked topsoil on the mostly extraordinarily steep slopes of the mountains. A vegetation cover composed of bushes, bracken and herbs accumulates much less biomass and weight than

a dense forest of 10–25m-high trees. In addition, the closely interwoven rhizome system of bracken that permeates the soil down to a depth of 1 m stabilizes the endangered layer of the soil.

Tree species characteristic of the former primary forests are very rarely found in the bracken-bush vegetation of the abandoned pastures, and therefore a swift regeneration of forest is very unlikely. Several reasons for the lack of forest species in the bushland are evident. The regenerative pressure of the bushes, which produce immense amounts of wind-dispersed seeds, by far outstrips that of the forest trees, the seeds and fruits of which are dispersed predominantly by birds and bats (Matt 2001). A single seed that has been dropped by a bird on the bushland has hardly any chance of germination. In addition, a substantial seed input from forest trees is unlikely due to the fact that the primary forest remnants are usually a great distance away (Fig 5). However, it cannot completely be ruled out that a secondary forest may slowly develop on areas where the abandoned pastures border the natural forest, or in the moister *quebradas*, where a few individuals of forest tree species may survive the repeated fires and where growth of the fern rhizomes is impaired (Brown 1986) due to waterlogged soil. However, apart from these specific situations natural forest recovery is very unlikely due to the combined effects of the factors mentioned above that prevent the establishment of trees in bushland (Fig. 6). Re-forestation with suitable tree species appears to be the only possible way to reconvert the fallow areas into sustainably exploitable land.

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