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Effect of forest clear-cutting on subtropical bryophyte communities in waterfalls, on dripping walls, and along streams

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Abstract. Forested freshwater ecosystems worldwide are threatened by a number of anthropogenic disturbances, such as water pollution and canalization. Transient or permanent deforestation can also be a serious threat to organisms in forested watersheds, but its effects on different types of freshwater systems has been little studied. We investigated lotic bryophyte communities on rock and soil in subtropical cloud laurel forests on La Gomera Island in the Canary Islands, Spain, and asked whether the response to forest clear-cutting varied among the communities associated with dripping walls, streams, and waterfalls. We compared three successional forest stages: ancient forests (>250 years), young forests (20–50 years after clear-cutting), and open stands (5–15 years after clear-cutting). In each of 56 study sites we sampled general vegetation and substrate data in a 0.01-ha plot and took composition data of bryophyte species in $3 + 3$ subplots of 1×1 m. The general pattern of decline in species richness and change in species composition after forest clear-cutting was stronger for streamside assemblages compared to assemblages on dripping walls and in waterfalls. The change in species numbers on rocks was larger than that on soils, because a guild of species growing on soil (but not on rocks) were favored by disturbance and thus increased in the disturbed sites. Most of the sensitive species could be classified as typical laurel forest species. Mosses were generally more tolerant to forest clear-cutting than were liverworts. We suggest that streamsides are more sensitive to disturbance than waterfalls and dripping walls because of a larger variation in microclimate before than after clear-cutting and because they are more easily invaded by early-successional species (both bryophytes and highly competitive vascular plants). We propose that special care should be taken along small streams within disturbed watersheds if bryophyte assemblages and threatened species should be protected. The susceptibility to anthropogenic pressures is probably rather high in ecosystems that do not regularly experience large-scale stand-replacing disturbances, especially on oceanic islands because of isolation and a small total habitat area for focal organisms.

Key words: Canary Islands, Spain; clear-cutting; disturbance; dripping wall; habitat loss; laurel forest; liverwort; moss; riparian environment; stream; substrate; waterfall.

INTRODUCTION

Knowledge on how communities of plants and animals respond to human-induced habitat modifications at varied spatial and temporal scales is fundamental for developing suitable management policies (Lindenmayer et al. 2006, Pressey et al. 2007). Running freshwater ecosystems are among the most disturbed global environments (Malmqvist and Rundle 2002). Deforestation of riparian systems is one important human activity that globally threatens populations of both aquatic and riparian taxa (Benstead et al. 2003, Hylander et al. 2005, Lorion and Kennedy 2009). Studies of the manner in which plants respond to anthropogenic stand-replacing disturbances in riparian systems have focused on particular environments such as streams and springs (Elliott et al. 1997, Heino et al. 2005, Dynesius et al. 2009). Although dripping walls (i.e., relatively vertical systems in which thin water films flow over rock faces) and waterfalls are recognized as regional biodiversity resources for invertebrates (Meyer and Wallace 2001, Ward et al. 2002, Collier and Smith 2006), little is known about their other organisms (e.g., plants) and their responses to stand-replacing disturbances. As the biotic responses to forestry might vary among types of freshwater systems, we here present a study comparing three key lotic environments: waterfalls, dripping walls, and streams. The study focused on the effect of forest clear-cutting on bryophyte communities in cloud laurel forests on La Gomera Island, Canary Islands, Spain.

Oceanic island ecosystems may be more sensitive to anthropogenic disturbances than ecosystems on continents for several reasons. First, long-term evolutionary history has in many cases resulted in a high level of endemism in such ecosystems (Whittaker and Fernández-Palacios 2007). Second, due to their small

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size and strong isolation, insular populations run a higher risk of extinction and have a lower chance of recolonization after catastrophic events (Whittaker et al. 2001, Gillespie et al. 2008). Third, regular large-scale disturbances (e.g., fires or insect outbreaks) are less common on islands, because of their isolation (Whittaker 1995, Brooks et al. 2002, Komdeur and Pels 2005), implying that species on islands might be more vulnerable to large-scale human-induced disturbances such as clear-cutting. This may be particularly true in subtropical regions where certain extreme weather phenomena, such as hurricanes, are also rare (Whittaker 1995).

The Canary Islands belong to the Macaronesian archipelagos that fall within the Mediterranean basin biodiversity hotspot (Myers et al. 2000). This status is largely related to their subtropical, evergreen (laurel) forests that harbor high diversity for a broad variety of taxonomic groups. Canarian forest riparian environments play an essential role in the insular hydrological cycle recharging water reservoirs (Hughes and Malmqvist 2005) and support abundant species-rich communities of bryophytes and invertebrates with high ratios of endemism (Malmqvist et al. 1995, González-Mancebo et al. 2008*a*). Natural large-scale disturbances are unknown, but small-scale disturbances such as treefall gaps and seasonal floods regularly occur with low extent and frequency, respectively (Hughes and Malmqvist 2005, Arévalo and Fernández-Palacios 2007).

Pressures from different long-term land uses (e.g., urbanization, water diversion, and forest clear-cutting) have resulted in a dramatic degradation in the integrity and quantity of the forested freshwater systems in the Macaronesian archipelagos, particularly in the Canaries (Beyer 1993, Malmqvist et al. 1995, Patiño et al. 2009). Indeed, most forested riparian systems in the Macaronesian region present a secondary successional stage, are still threatened by forestry, flow regulation, and agriculture, and are not included in protected reserves (Malmqvist et al. 1995, Hughes and Malmqvist 2005). There is thus an urgent need to understand how riparian communities respond to habitat loss and modifications due to human activities (Reeves et al. 2006) such as clear-cutting in laurel forest landscapes.

Forest clear-cutting impacts freshwater ecosystems, modifying hydrological processes and physical-chemical conditions (Brosofske et al. 1997, Boothroyd et al. 2004), for example by decreasing interception and groundwater recharge (Fahey and Jackson 1997, Gabriel and Jauze 2008). Insolation, temperature, humidity, and soil moisture also differ significantly between forested riparian zones and open clear-cut riparian stands (Brosofske et al. 1997, Boothroyd et al. 2004). This may severely modify habitat availability and landscape connectivity, impacting biodiversity and ecological processes (Naiman et al. 1993, Bragg 2000, Lindenmayer et al. 2006).

Bryophytes may be one of the taxonomic groups that are particularly sensitive to clear-cutting due to their poikilohydric nature (Patiño et al. 2009), which limits their control over water uptake and loss (During 1992). Even specimens that survive mechanical effects of clear-cutting may not tolerate indirect effects, such as the drier conditions found in clear-cut areas (Fenton et al. 2003, Åström et al. 2007). This may be particularly true for late-successional species with narrow environmental requirements because of the drastic change in microclimate and often availability of (micro-) habitats (Frego 2007, Dynesius et al. 2009, Patiño et al. 2009). Earlier studies on bryophyte responses to forestry have highlighted a large variation in species responses mediated by the type of environment (Pharo et al. 2004, Heino et al. 2005). For instance, substrate form and associated microclimate were important factors explaining the magnitude of clear-cutting effects, as bryophytes on concave substrates were more resilient than those on convex surfaces in boreal streamside forests (Hylander et al. 2005, Dynesius and Hylander 2007). Similarly, bryophytes in streamside forests were less sensitive to clear-cutting than bryophytes in upland habitats (Dynesius et al. 2009). However, streamside forests might be more susceptible to long-term species losses as they contain many species that are not found elsewhere in the landscape. These findings are from boreal and temperate zones that experience seasonal variation in climate, but might be more relevant in subtropical (and tropical) regions in which species are adapted to a humid and relatively stable climate throughout the year.

Our study provides an assessment of bryophyte responses to forest clear-cutting that integrates multiple and previously unexplored freshwater habitats by comparing dripping walls and waterfalls with streamside environments. This was done in 56 sites distributed among three successional forest stages after clear-cutting: ancient (laurel) forest stands, young (laurel) forest stands, and newly clear-cut stands. In the Macaronesian lotic environments, bryophytes typically inhabit rocks and soils in streamsides at or immediately above the air–water interface, while they usually occur in both submerged and emerged substrates in waterfalls and on dripping walls (González-Mancebo et al. 2008*a*). We asked whether the bryophyte communities in the three habitats and on the two major substrates (rock and soil) differed in their responses to clear-cutting. We also examined whether bryophytes of different species groups (classified according to phylogeny, conservation status, endemism, habitat preferences, and main distribution patterns) responded differently to forest clear-cutting. We hypothesized that the moister/wetter substrates of dripping walls and waterfalls compared to streamside environments would moderate species loss and change in community composition after clear-cutting.

TABLE 1. Environmental variables (means, with range in parentheses) among the 56 study sites on La Gomera, Canary Islands, Spain, according to the successional forest stages and the freshwater environment types.

	Ancient forest stands			Young forest stands
Variables	Dripping wall ($n = 9$)	Stream ($n = 8$)	Waterfall ($n = 7$)	Dripping wall ($n = 5$)
Altitude (m)	**891.3** (692–1160)	**988.1** (860–1150)	**912.9** (690–1150)	705 (560–855)
Slope (°)	**86.7** (80–90)	24 (0–85)	**87.1** (75–95)	81 (60–90)
Aspect (°)	1 (1)	**1.1** (1–2)	1 (1)	1 (1)
Rock cover (%)	84.4 (80–90)	61.9 (20–95)	**98.6** (90–100)	85 (70–90)
Rock size†	4 (4)	3.3 (2–4)	4 (4)	4 (4)
Soil cover (%)	15.6 (10–20)	**38.1** (5–80)	1.4 (0–10)	15 (10–30)
Soil size†	1 (1)	**1.2** (1–2)	0.1 (0–1)	1 (1)
Channel width (m)	**6.6** (11–4)	2.6 (1–5)	2.5 (0.5–6)	**6.6** (3–10)
Wet substrate (%)	91.1 (80–100)	63.1 (40–80)	**97.1** (90–100)	**92** (80–100)
pH	7.4 (6.7–7.5)	7.2 (6.8–7.5)	7.4 (7.0–7.6)	7.6 (7.4–8)
NO_{3-} (g/mL)	1.1 (0–5)	0 (0)	0 (0)	10 (0–40)
PO_{4-} (g/mL)	0 (0)	0 (0)	0 (0)	0 (0)
Laurel dbh (cm)	**78.4** (63.2–91.2)	**76.1** (63.7–87.1)	**62.8** (35.4–78.6)	25.2 (31.4–20.5)
Forest height (m)	**19** (15–25)	**20** (12–25)	**18** (12–25)	7 (5–8)
Tree species richness (no./plot)	**3.8** (2–6)	**4.4** (3–6)	**3.4** (2–5)	3.2 (1–5)
Tree cover (%)	**63.9** (105–21)	**82.6** (60–118)	**78.6** (70–90)	17 (10–27)
Shrub species richness (no./plot)	1.2 (0–3)	0.4 (0–1)	1.6 (1–3)	**2.8** (1–5)
Shrub cover (%)	10.3 (0–30)	0.3 (0–1)	3.6 (0.5–10)	**37.6** (15.2–55)
Grass species richness (no./plot)	1.3 (0–4)	1.6 (0–5)	0.9 (0–2)	**5.4** (2–8)
Grass cover (%)	2.2 (0–5)	4.4 (0–15)	5 (0–20)	27.6 (6–45)
Fern species richness (no./plot)	**3.1** (2–5)	**1.7** (1–2)	1 (0–2)	1.4 (1–2)
Fern cover (%)	**28** (8–85)	**6.7** (3–15)	3.3 (0–6)	6.6 (1–15)
Vascular species richness (no./plot)	9.4 (6–13)	8.1 (5–11)	6.9 (4–9)	**12.8** (7–17)
Vascular species cover (%)	**104.3** (62–163)	**94.1** (71–124.5)	80.5 (78–105.5)	88.8 (72–102)

Notes: Sample size (number of 0.01-ha plots in each combination of habitat and successional stage) is provided in parentheses in the column headings. The Kruskal-Wallis H test was used to explore significant ($P < 0.05$) differences among successional forest stages. The three highest values of each variable appear in boldface.

† For more information on these qualitative variables see *Methods*.

METHODS

Study area

The study was conducted in subtropical cloud laurel forest landscapes on La Gomera, Canary Islands, Spain (Appendix A; also see Plate 1). The selected area has a mean annual temperature ranging from 13° to 17°C and a mean annual rainfall ranging from 700 to 900 mm, with a major additional water supply deposited by fog depending on season, altitude, and topography (Pérez de Paz 1990, Marzol 2008). Natural riparian forests are dominated by the tree species *Laurus novocanariensis* and *Persea indica* and the shrubs and ferns *Gesnouinia arborea*, *Pericallis appendiculatus*, and *Diplazium caudatum*. Young forest and lotic riparian sites without forest cover are usually dominated by dense patches of *Salix canariensis*, the shrubs *Arundo donax* and *Rubus* spp., and the herbs *Tradeschantia fluminensis* and *Lemna minor* or the horsetail *Equisetum ramosissisum* (Pérez de Paz 1990, Del Arco et al. 2009).

La Gomera Island currently maintains one of the most diverse and largest laurel forest formations in the Macaronesian region (Del Arco et al. 2009) as well as a high number of freshwater systems, due primarily to the fact that a large area of the central island is protected by the Garajonay National Park (Appendix A). Many adjacent areas, however, including some stands within the National Park, have been clear-cut during the last 70 years. Some of these stands have been left for natural forest regeneration, while others have been kept open during the last 20 years because of the features of the lotic environment (e.g., vertical substrates) or anthropogenic activities (e.g., riparian zones managed for agriculture).

Study design

We considered three types of freshwater systems: dripping walls, streams, and waterfalls. The initial selection included sites with three successional stages following clear-cutting (i.e., ancient forest, young forest, and open stands), which had to fulfill the following criteria: (1) ancient forest stands >250 years old; (2) young forest stands clear-cut 20–50 years ago; (3) open stands clear-cut 5–15 years ago and still in an open state due to natural conditions; (4) no human water extraction from the watercourse; and (5) no adjacent, recent forestry activities (>50 m from the freshwater environment). Ages of ancient forest stands and years since clear-cutting were supplied by landowners and the local Forest Guard Board of the Garajonay National Park.

During the years 2004–2005, we visited potential sites and checked that (1) the site presented a lotic environment with a permanent water flow throughout the year (seasonally wet sites were avoided); (2) there was no direct influence of other human-induced disturbances (e.g., grazing); (3) sites were surrounded by the same successional forest stage with a minimal size

Table 1. Extended.

Young forest stands		Open stands			K-W test	
Stream ($n = 5$)	Waterfall ($n = 6$)	Dripping wall ($n = 6$)	Stream ($n = 7$)	Waterfall ($n = 3$)	*H*	*P*
681.2 (555–785)	680.8 (530–855)	745.8 (555–920)	856.2 (770–905)	665 (600–740)	21.9	**<0.001**
19 (5–35)	**85** (80–90)	77.5 (45–95)	4 (2–5)	76.7	5.1	0.076
1 (1)	1 (1)	1 (1)	1 (1)	1 (1)	1.3	0.515
61 (40–90)	**93.5** (70–100)	81.7 (35–95)	35.7 (20–70)	**98.3** (95–100)	1.7	0.419
2.6 (1.7–3.6)	4 (4)	4 (4)	2.1 (1.5–3.3)	4 (4)	2.6	0.262
39 (10–60)	6.5 (0–30)	18.3 (5–65)	**64.3** (30–80)	1.7 (0–5)	1.1	0.419
1.2 (1–2)	0.5 (0–1)	1 (1)	**1.2** (1–1.5)	0.3 (0–1)	0.5	0.753
2.4 (1.5–3.5)	1.6 (0.5–3)	**6.3** (4–9)	2.3 (1.5–3.5)	**3.3** (1–7)	1.1	0.593
66.6 (60–75)	**94.1** (90–100)	88.3 (80–100)	61.4 (50–70)	91.7 (85–100)	1.5	0.414
7.7 (7.5–8)	7.7 (7.4–8)	7.5 (7.0–8.2)	**7.8** (7.6–8.2)	**7.8** (7.4–8.2)	11.1	**0.004**
20 (0–40)	15 (0–40)	18.3 (0–60)	**26.4** (5–60)	**21.7** (0–60)	24.5	**<0.001**
0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	…	…
32.3 (16.9–41.3)	24.3 (16.3–38.1)	6.8 (0–12)	0 (0)	3.7 (0–11)	47.8	**<0.001**
10 (7–16)	9 (3–20)	3 (0–5)	0 (0)	2 (0–7)	43.8	**<0.001**
2.6 (1–5)	2.3 (1–5)	1.2 (0–4)	0 (0)	0.3 (0–1)	30.2	**<0.001**
33.4 (15–57)	46.3 (90–26)	1.3 (0–5)	0 (0)	1.7 (0–5)	42.9	**<0.001**
2.8 (2–3)	1.7 (1–3)	**2.3** (1–4)	2 (1–3)	1.7 (0–3)	17.2	**0.001**
45.7 (5–74)	22.7 (5–50)	26.7 (5–50)	**32.5** (6–55)	8.3 (0–15)	25.7	**<0.001**
5.2 (1–13)	2.8 (1–8)	**6.5** (1–9)	**5.7** (3–9)	4.7 (1–7)	24.4	**<0.001**
36.6 (4–84)	12.4 (1–41)	**34.3** (1–85)	**51.3** (11–67)	33.7 (18–43)	28.5	**<0.001**
1.8 (0–4)	1 (0–2)	0.5 (0–2)	1.3 (1–2)	0.3 (0–1)	12.9	**0.002**
9.2 (0–27)	5.7 (0–15)	4.2 (0–15)	2.3 (0.5–7)	1.7 (0–5)	12.7	**0.021**
12.2 (5–16)	7.8 (5–17)	**10.5** (5–15)	8.9 (6–13)	7 (1–11)	2.8	0.244
102.5 (84–125)	86.9 (61–111.5)	69 (17–131)	46.5 (21–83)	45.3 (38–58)	17.5	**0.002**

of 3 ha; and (4) there were no large differences in slope and cover of soil and rock (considering each lotic environment separately). Altogether, 56 sites fulfilled the criteria (Table 1; Appendix A): 20 dripping walls (nine ancient forests, five young forests, and six stands without canopy cover), 20 streamside environments (eight ancient, five young, and seven open stands), and 16 waterfalls (seven ancient, six young, and three open stands).

The present study may be considered as a chronosequence, which is an approach commonly used in ecological studies for slow ecological processes such as forest succession. However, space-for-time substitutions exhibit particular disadvantages, such as possible small differences between stands with regard to site history or edaphic and microclimatic conditions (Foster and Tilman 2000, Johnson and Miyanishi 2008). Being aware of such limitations, chronosequence-based studies have been found to be useful for studying successional gradients, not least in forest ecosystems (Foster and Tilman 2000, Johnson and Miyanishi 2008, Patiño et al. 2009).

Environmental properties

The study sites were located in the central part of La Gomera from ~550 to 1100 m above sea level (Appendix A; Table 1). Each study site included one plot of 0.01 ha (normally 10 × 15 m, but sometimes with different shape depending on structural features of the environment). In each site, we randomly located a plot midpoint with respect to the midpoint of the water channel (e.g., the plot fitted longitudinally along streams with the channel entirely inside the plot). In dripping walls and waterfalls, about half of the plot was placed in the vertical substrate and the remaining 50% on the relatively horizontal floor. The following environmental variables were gathered from each 0.01-ha plot: altitude, slope, and orientation. From the lower plot side, channel widths were measured every meter at 10 sections perpendicular to the direction of the water flow. The percentage of permanently wet substrate in each plot was estimated by eye. In order to characterize other abiotic features of the study area, previous limnological studies (Beyer 1993; A. Fernández-López, *unpublished data*) were used to obtain plot-wise information on pH and concentrations of nitrates and phosphates.

The size and cover of rocks and soils (i.e., smaller substrates on relatively stable surfaces) were estimated in each site. Rock size was grouped into four classes, and the cover of each class was estimated by eye: (1) walls (or material >3 m in diameter that would rarely be moved by the water); (2) boulders (1–2.9 m); (3) medium rocks (0.2–0.99 m); and (4) small rocks (0.05–0.19 m). Similarly, soil cover was visually grouped into two size classes: (1) small stones/gravel (10–49 mm) and (2) small gravel/sand (<9 mm). In each plot, tree height and canopy cover (as a percentage) were visually estimated, as well as cover of shrubs, grasses, ferns, bryophytes, and total vascular plants. All tree stems (>20 cm) were measured (diameter at the breast height, dbh, measured at 1.3 m above the ground surface), counted and identified at the species level; shrubs, grasses, and ferns were also identified (Table 1). Nomenclature follows

Acebes et al. (2004) for vascular plants and González-Mancebo et al. (2008*b*) for bryophytes.

Bryophyte sampling

A total of 12 subplots, 1 m^2 each, were placed in each 0.01-ha plot. Six subplots, three on rocks and three on soils (the main bryophyte substrates in these environments; González-Mancebo et al. 2008*a*), were systematically placed at every meter (except for waterfalls, where only rocks were investigated due to their low soil cover). The subplots in streams were placed along the direction of the water flow, with 20% of the total area within the water channel (including submerged substrates) and the remaining 80% placed along the riparian zone. On dripping walls and in waterfalls, the subplots were also systematically placed, but perpendicular to the direction of flow and as high as possible ($>$1.5 m above the relatively horizontal floor). Another set of three 1-m^2 subplots for each type of substrate were subjectively placed in locations within the plot that displayed the highest bryophyte cover; the aim was to ensure that as many species as possible at each 0.01-ha plot were recorded (all the subplots had to be $>$1 m apart). The data from the subjected subplots were only used for the species list (see Appendix B) and for the analysis of the relative difference in the number of species (per 0.01-ha plot) among the successional forest stages. In the remaining analyses, the plot-level richness was always calculated from the three systematic 1-m^2 subplots (i.e., the species from the three subplots were pooled or their mean calculated). In each subplot, we estimated the cover (as a percentage) of each bryophyte and vascular plant species. We collected many small bryophyte samples to ensure correct identification of species in the laboratory. Voucher specimens were deposited in the TFC herbarium of La Laguna University.

Ecological classification of species

We analyzed subgroups of species classified according to phylogeny (liverworts and mosses), conservation status, endemism, habitat preferences, and main pattern of distribution. The category of red-listed species was based on the work of J. M. González-Mancebo and A. Fernández-López (*unpublished manuscript*), who have recently elaborated the red list of bryophytes for the Canary Islands following the criteria laid out by the International Union for the Conservation of Nature and Natural Resources (IUCN). Data on endemism included Iberian-Macaronesian, Macaronesian, and Canarian endemisms (González-Mancebo et al. 2008*b*). All bryophyte species were classified with respect to the degree of affinity to freshwater environments based on personal observation and literature (González-Mancebo et al. 2004, 2008*a*). Thus, bryophyte species were classified as "characteristic" if they mainly occur in streams or other water bodies (e.g., *Aneura pinguis*, *Dumortiera hirsuta*, *Fissidens coacervatus*, *Tetrastichium fontanum*). A species was classified as "facultative" if the main habitat association is related to emerged environments, although it may appear in freshwater systems (e.g., *Rhynchostegiella trichophylla*, *Fissidens serrulatus*). "Occasional" taxa have their main distribution in non-freshwater environments or on other substrates than those investigated (e.g., trees), whose presence on rock and soil in freshwater systems is accidental or circumstantial (e.g., *Isothecium myosuroides*, *Didymodon vinealis*, *Fissidens bryoides*).

We also analyzed ecological subgroups of species according to their main distribution pattern (in relation to precipitation, altitude, slope, and vegetation in the Canaries). La Gomera Island can be divided into different bioclimatic belts characterized by a certain combination of abiotic and biotic conditions. The so-called "Thermo-Mediterranean belt" is the area with a generally humid climate in the middle levels of the island (Del Arco et al. 2009). Based on personal observation and on the literature (González-Mancebo et al. 2008*b*), we classified each species as follows: "laurel forest" species that are generally associated with forests in the "Thermo-Mediterranean belt" (e.g., *Acanthocoleus aberrans*, *Thamnobryum alopecurum*); "humid bioclimatic belt" species, occurring in the same area but not restricted to forests (e.g., *Asterella africana*, *Marchantia polymorpha*); and "nonrestricted" species, which often occur also outside the "Thermo-Mediterranean belt" (e.g., *Ptychostomum* spp., *Tortula* spp., *Didymodon* spp.). The ecological categories for each species are shown in Appendix B.

Data analysis

We analyzed differences in environmental variables among the successional forest stages (i.e., ancient forests, young forests, and open stands) using nonparametric Kruskal-Wallis tests, because most variables were not normally distributed. Correlation analyses (Spearman's rank correlation) were performed to describe relationships among the variables measured in each 0.01-ha plot. These correlations were also made for each successional forest stage separately (not shown), obtaining similar results to the previous general analyses.

Cover data for the three systematic 1-m^2 subplots were used in all multivariate analyses. The differences in species composition among the combinations of freshwater habitats (dripping wall, stream, and waterfall) and substrates (rock and soil) along the successional forest gradient were analyzed in two steps. First, we conducted a two-dimensional nonmetric multidimensional scaling analysis (NMDS; Clarke 1993) on the ancient forest sites to explore whether there were any differences in community composition among the different lotic habitats. An inspection of the ordination plot for rocks indicated that the species composition of waterfalls and dripping walls was similar, while streams differed from those environments. Thus, data from the rocks of waterfalls and dripping walls were pooled in the further analyses. The ordination plot for species on soils in the ancient forests also showed that dripping walls and streams differed; therefore, they were also analyzed separately.

To test for differences in community composition for each combination of freshwater environment and substrate across the successional forest gradient (here, the grouping variable), we used a multiple response permutation procedure (MRPP; Mielke and Berry 2001) in PC-ORD (McCune and Mefford 1999). The MRPP is a nonparametric method that tests for differences in species composition between two or more defined groups (McCune and Grace 2002). We report MRPP's test statistic (T and its associated P value), which describes the separation between groups (i.e., most negative T indicates strongest separation), and MRPP's chance-corrected within-group agreement value (A), which describes the effect size or degree of within-group homogeneity compared to the random expectation (i.e., A attains its maximum value of 1 when all items are identical within groups; McCune and Grace 2002). We ran MRPP on a rank-transformed distance matrix with the Sorensen (Bray-Curtis) distance measure and the n/sum(n) weighting factor (where n is the number of items in the group).

For each combination of environment and substrate, the variation in species composition across the successional forest gradient was visualized using NMDS (Clarke 1993). The goodness of fit of the two-dimensional design of the rank dissimilarities was measured by the "stress" value (i.e., an inverse measure of the fit of the data in two dimensions, indicating how faithfully the high-dimensional relationships among the plots are represented in the two-dimensional ordination plot; McCune and Grace 2002). As in MRPP, NMDS was performed on Bray-Curtis dissimilarity matrices of species (abundance-based; the mean cover of each species in the three systematic subplots) in PRIMER 6 PERMANOVA + β 12 (Anderson et al. 2008). The data were fourth-root transformed before analyses to reduce the weight of common species in all the analyses (Clarke and Warwick 1994).

In order to determine whether individual species showed preferences for specific successional forest stages, we used the indicator species analysis (ISA) approach of Dufrêne and Legendre (1997) in PC-ORD software (McCune and Mefford 1999). In the ISA, each species gets an indicator value for (in our case) ancient forests, young forests, and open clear-cut stands in a procedure that involves both the relative abundance and frequency of each species (McCune and Grace 2002). The ISA values range from 0 (no presence of a species in a given successional stage) to 100 (perfect indication) in each stand type, and a relatively high indicator value (≥ 25) is given to a species that is abundant and frequently found in a specific successional forest stage (Dufrêne and Legendre 1997). For each species a Monte Carlo permutation test was used to determine whether the maximum indicator value was significantly different from the values in the other groups. We did one analysis on the three successional stages separately and another further analysis in which the young and open stands were pooled.

After the second analysis (with the pooled stages), we calculated ISA values for individual species in each combination of environment and substrate and then the mean for each species, in case it occurred in several combinations (see Appendix B). By subtracting each species' ISA value for ancient forest stands from the value for disturbed sites (pooled young forest stands and open stands), we obtained, for each species, a positive value if it was associated with disturbed stands and negative if it was associated with ancient forest stands. Input data were the same as in the NMDS and MRPP analyses. We compared the distribution of the differences in ISA values among and within each ecological group using a Kruskal-Wallis test or a Mann-Whitney U test, respectively.

The differences in bryophyte richness (i.e., the number of species from the three systematic 1-m^2 subplots were pooled) among the successional forest stages for each combination of environment and substrate were explored using a two-way analysis of covariance (ANCOVA). Because pH and water availability have been recognized as key factors in explaining the distribution of freshwater bryophytes (Hylander and Dynesius 2006, Dynesius et al. 2009) and because there was a strong correlation between altitude and most variables related to the successional stage (except for cover of grasses; Appendix C), the variables pH, permanently wet ground, altitude, and grass cover were initially included as covariates. The type of lotic environment and successional forest stage were included as fixed factors. All the covariates were transformed as $\log_{10}(x)$ or $\log_{10}(x + 1)$ to standardize variances and improve normality. We subsequently tested for homogeneity of variances using Levene test. We excluded first-interaction terms stepwise and then covariates if they were not statistically significant ($P < 0.05$), starting with the least significant until only significant interactions and co-variables were left (Underwood 1997). The Spearman correlations, Kruskal-Wallis H test, Mann-Whitney U test, and ANCOVA were implemented in SPSS version 17.0 (SPSS 2009).

RESULTS

Site characteristics across the successional forest gradient

The majority of environmental variables were significantly different among groups of sites pooled according to the successional forest stage (Table 1). The dbh of laurel tree species, forest height, richness and cover of tree species, and altitude were significantly higher in ancient forests. Young forests were different regarding richness and cover of shrubs. Clear-cut stands showed the highest values of pH, NO_3^-, and richness and cover of grasses. Although not significantly different among

TABLE 2. Results of the multi-response permutation procedure analyses (MRPP) of bryophyte communities grouped according to a combination of freshwater environments and substrates, with pairwise comparisons using the three successional forest stages.

	Global test		Ancient forest vs. young forest stands		Ancient forest vs. open stands		Young forest vs. open stands	
Community	T (A)	P	T (A)	P	T (A)	P	T (A)	P
Rocks								
Dripping wall–waterfall†	−5.54 (0.05)	**<0.001**	−3.57 (0.04)	**0.035**	−5.07 (0.06)	**0.001**	−1.39 (0.02)	0.114
Streamside	−7.34 (0.17)	**<0.001**	−6.11 (0.19)	**<0.001**	−7.15 (0.11)	**<0.001**	−3.87 (0.09)	**0.017**
Soils								
Dripping wall	−2.48 (0.04)	**0.021**	−1.53 (0.03)	0.081	−3.35 (0.06)	**0.008**	1.99 (−0.01)	0.992
Streamside	−3.28 (0.04)	**0.009**	−2.16 (0.02)	**0.041**	−3.82 (0.05)	**0.001**	−1.62 (0.04)	0.067

Notes: T is the separation test statistic; A is the chance-corrected within-group agreement; significant differences at $P < 0.05$ appear in boldface. The number of plots in each combination of habitat and successional stage is provided in Table 1.

† Dripping wall and waterfall plots were combined because they displayed high similarity in the ancient forest stands (MRPP, $T = -1.45$, $A = 0.022$, $P = 0.095$), as also seen in the ordination patterns from a nonmetric multidimensional scaling (not shown).

the successional stages (Table 1), cover and size of rocks, permanently wet substrate, and channel width were higher in dripping walls and waterfalls, whereas cover of vascular plants and cover and size of soils were higher in streams. Altitude was positively correlated with laurel tree species dbh, forest height, and richness and cover of trees, but negatively with richness and cover of shrubs, NO_3^-, and pH (Appendix C).

Changes in species composition

The species composition differed significantly among the successional forest stages, for all the combinations of environment and substrate (MRPP; Table 2), as illustrated by the separation of sites in the ordination space (NMDS; Fig. 1). The significant values of the MRPP's test statistics (T and A) for the rocks and soils along streams, however, were generally higher than those found for the rocks and soils, respectively, in the other environments (Table 2). Species composition of young forest and open sites only differed significantly on rocks in streamside sites (Table 2), which is also indicated by the slight separation of the sites in the ordination space (Fig. 1b, d). Except for rocks along streams, all the combinations of environment and substrate had a wide within-group variation ($A < 0.09$; McCune and Grace 2002).

Liverworts, red-listed species, and laurel forest species generally had a negative association with ancient forests as shown by the fact that the difference in ISA values between ancient forests and the pooled young forest and open stands within each group differed significantly from zero (Mann-Whitney U test, $P < 0.05$; Fig. 2). For instance, species such as the liverworts *Acanthocoleous aberrans* (mean difference in ISA value = –15.0; Appendix B), *Dumortiera hirsuta* (–62.7), and the mosses *Homalia webbiana* (–12.0), *Rhynchostegiella macilenta* (–16.0), *Tetratichium fontanum* (–34.5), and *Thamnobryum alopecurum* (–44.3), all classified as laurel forest species and red-listed species, were more strongly affiliated with ancient forests than with open stands and young forests (Table 3).

The guilds of species classified by their affinity to freshwater habitat, as well as mosses, endemics, humid belt species, and nonrestricted species, did not display a clear association with either ancient forest or the pooled group of young forest and open stands (Fig. 2). In other words, the differences in the mean ISA values for these groups did not differ significantly from 0 (Mann-Whitney U test, $P > 0.05$), although many of individual species were strongly associated to at least one of the groups. Accordingly, many species had a positive ISA value (Appendix B). The humid bioclimatic belt liverworts such as *Asterella africana* (mean difference in ISA value = +15.0) and the bioclimatically nonrestricted mosses such as *Eucladium verticillatum* (+14.3) and *Rhychostegiella litorea* (+9.0) are some such examples, with high ISA values in different disturbed stages and environments (Table 3).

The differences found along the streams between young forests and open clear-cut stands (Table 2) are related to the prevalence of species such as *Asterella africana*, *E. verticillatum*, *R. litorea*, and *Sciuro-hypnum plumosum* in the young forest stands (Table 3), whereas a subset of drought-tolerant taxa, such as *Bryum argenteum*, *B. torquescens*, *Didymodon vinealis*, and *Fissidens bryoides* typified the open stands (Table 3). Endemics such as *Fissidens coacervatus* and *Rhynchostegiella trichophylla* or the nonrestricted mosses *Tortella nitida* and *Tortula solmsii* typified the dripping walls and waterfalls in young forest stands (Table 3), while *Ptychostomum capillare* and *Marchantia polymorpha* were more strongly associated with those environments in open clear-cut stands (Table 3).

Changes in species richness

A total of 86 bryophyte species (30 liverworts and 56 mosses) were found in the 56 sites (Appendix B). In terms of number of species, dripping wall was the richest habitat for liverworts (25 species), while streamside was for mosses (42 species). These results should be considered cautiously because we sampled a smaller area in waterfalls because only one type of substrate

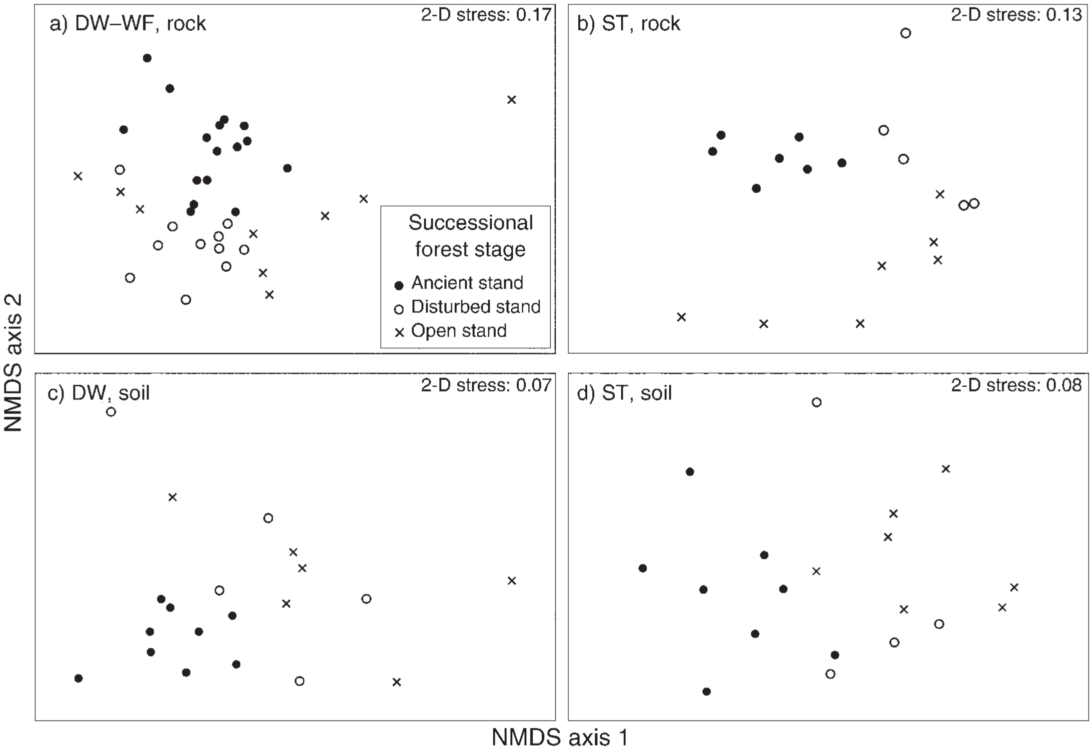

FIG. 1. Ordination plots showing site scores from two-dimensional nonmetric multidimensional scaling (NMDS) analyses of bryophyte species on (a) rocks in dripping walls and waterfalls (DW–WF), (b) rocks in streamside sites (ST), (c) soils in dripping wall sites (DW), and (d) soil in streamside sites (ST). The two-dimensional stress (2-D stress) is an inverse measure of the fit of the data in two dimensions, indicating how faithfully the high-dimensional relationships among the plots are represented in the two-dimensional ordination plot.

(rocks) could be surveyed in such an environment (see *Methods: Bryophyte sampling*). The total number of bryophyte species on rocks (i.e., the three systematic + three subjected 1-m^2 subplots were pooled) only differed significantly among successional forest stages of streams (Fig. 3a), where on average 19.8 species (per 0.01-ha plot) were found in ancient forest stands compared to 8.9 species (45% of the species in ancient stands) in young forests and 6.4 species (32.5%) in open clear-cut stands (Fig. 3a). The total number of species on soils (per 0.01-ha plot) did not differ significantly among successional stages, and there was almost the same number of species in ancient forests as in open stands (Fig. 3a). In contrast, the most distinctive species for ancient forests (i.e., with a significantly higher indicator value; Dufrêne and Legendre 1997) were significantly fewer in disturbed successional stages on rocky substrates (Fig. 3b). This difference, however, was slightly larger in streamsides, where on average 3.2 species per 0.01-ha plot were found in young forests (27.8% of the 11.5 distinctive species in ancient stands) and only 1.7 species in open clear-cut stands (6.1%). The difference in the number of ancient forest species on soils followed a similar pattern to that found on rocks, being slightly lower in open clear-cut stands along streamsides (Fig. 3b), with only 9.1% of the ancient forest species.

The numbers of liverwort species on rocks differed among the three different habitat types (dripping wall, waterfall, and stream) and the three successional forest stages (ancient forest, young forest, and open stands; Table 4). The highest richness of liverwort species occurred in ancient forests of the three freshwater environments (Fig. 4). The number of moss species on rocks in ancient forests was only significantly higher along streamsides (Fig. 4), with habitat type as a significant variable in the ANCOVA model (Table 4). Conversely, the number of liverwort and moss species on soils did not show significant differences among the three successional stages and habitat types (Table 3, Fig. 4). Altitude and amount of permanently wet ground (except for soil mosses) and cover of grasses for liverworts were statistically significant co-variables in all analyses (Table 4).

On rocks, the number of red-listed, endemic, facultative, and laurel forest species were higher in ancient than in open and young forest stands, whereas humid bioclimatic belt species only followed this pattern on streamsides (Fig. 4). Most red-listed taxa inhabiting rocks (e.g., *Jubula hutchinsiae*, *H. webbiana*, *T. fontanum*, and *T. alopecurum*) were exclusive to ancient forest stands (Table 3, Appendix B). In contrast, for soils only red-listed species on dripping walls and laurel forest

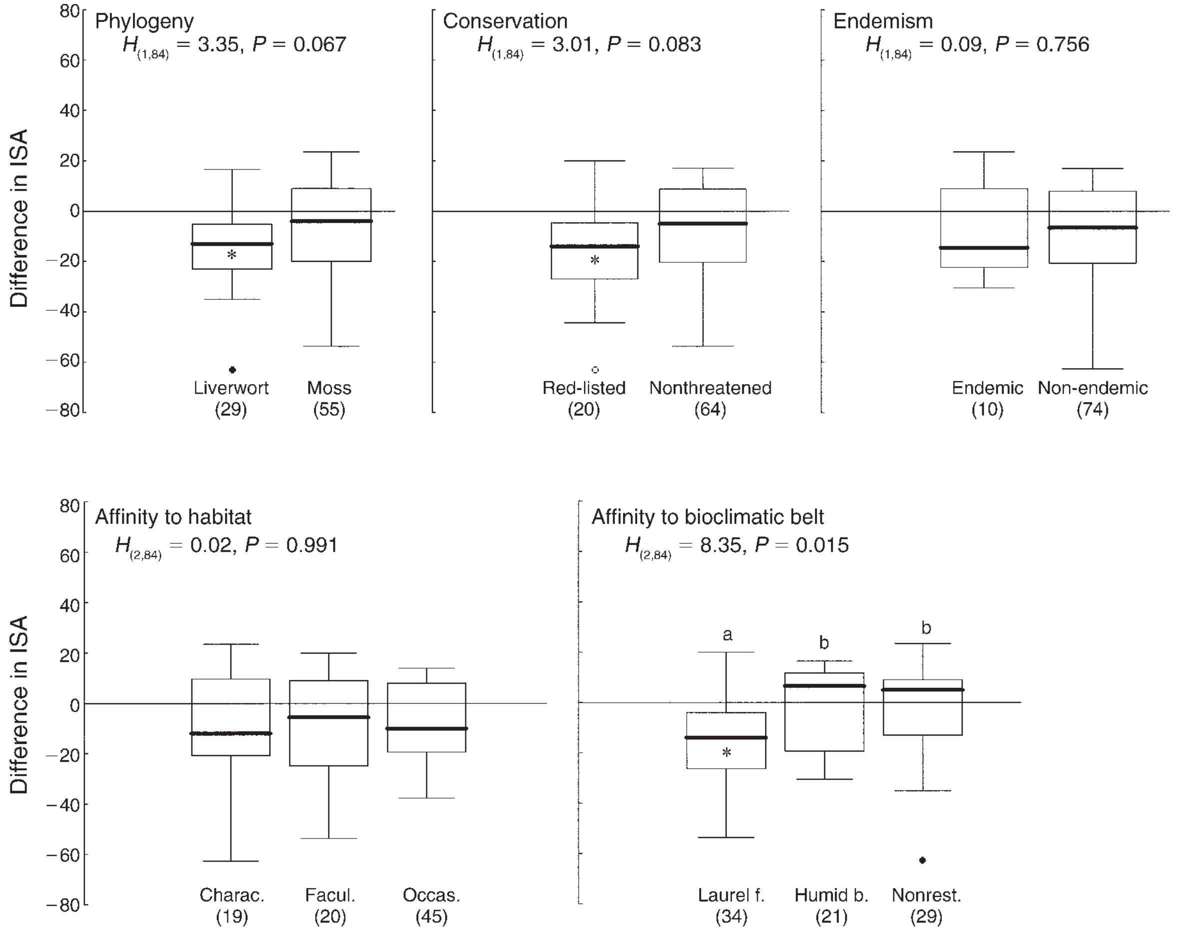

FIG. 2. Box plots illustrating the variation among species' response to deforestation. The response variable is the difference between a species' indicator value (according to indicator species analysis, ISA) in ancient vs. disturbed sites (young forest and open stands were considered together), summarized for the number of species indicated in parentheses below each box. Negative values denote species having higher indicator values for ancient forest than for young forest and open stands. Abbreviations are: Charac., characteristic species; Facul., facultative species; Occas., occasional aquatic species; Laurel f., laurel forest species; Humid b., humid bioclimatic belt species; Nonrest., nonrestricted species. The box contains 50% of the values (median indicated), the whiskers 95%, and the empty and full circles indicate observations outside this range (>1.5 and >3 times the box height, respectively). An asterisk denotes a significant ($P < 0.05$) difference between the mean and 0, while the P values are from comparisons among categories (Kruskal-Wallis H test and Mann-Whitney U test). Lowercase letters above bars indicate significant differences among groups.

species along streamsides and on dripping walls were significantly higher in ancient forest stands (Fig. 4). No group had significantly more species in disturbed stages than in ancient forest stands, except for the group of bioclimatically nonrestricted species (most mosses) in open stands along streams (Fig. 4e; Mann-Whitney *U* test, $P > 0.05$).

DISCUSSION

Our data show that the responses of freshwater bryophyte communities to clear-cutting varied depending on the type of environment (dripping wall, stream, and waterfall) and substrate (rock and soil). There was a general pattern of a lower number of species and a difference in species composition between ancient forests and both of the younger successional forest stages, emphasizing the importance of late-successional forests for many bryophyte species as also has been shown in other biomes (e.g., Pharo et al. 2004, Dynesius and Hylander 2007, Frego 2007; but see Gustafsson et al. 2004). In agreement with our hypothesis, stream assemblages seemed to be more sensitive to forest clear-cutting than those on dripping walls and waterfalls. Indeed, the streamside sites displayed more pronounced differences in species composition (i.e., larger separation between groups in the MRPP; see *T* values in Table 2) between ancient and younger successional stages and had a larger difference in species richness (mainly on rocky substrates) than open and young forest sites with dripping walls or waterfalls (Figs. 3 and 4). These findings emphasize the importance of understanding the mechanisms that control the variation

Table 3. A selection of distinctive species in the three successional forest stages.

Species	Phylogenetic group	Red list†	ISA value			
			Rocks in DW–WF	Rocks in ST	Soils in DW	Soils in ST
Ancient forest stands						
Acanthocoleous aberrans	L	yes	42	x	x	
Aneura pinguis	L	yes	x	x	31	
Cololejeunea schaeferi	L	···	x	61		
Dumortiera hirsuta	L	yes	77	83	76	34
Saccogyna viticulosa	L	···	56	x	49	x
Fissidens serrulatus	M	···	44	x	x	38
Homalia webbiana	M	yes	x	x	32	
Isothecium myosuroides	M	···	x	75	x	57
Oxyrhynchium hians	M	···	x	x	x	57
Rhynchostegiella macilenta	M	yes	x	69	x	
Tetrastichium fontanum	M	yes	44	x		
Thamnobryum alopecurum	M	yes	x	88	x	57
Young forest stands						
Aneura pinguis	L	yes	x	47	x	38
Asterella africana	L	···	x		35	50
Anomobryum julaceum	M	···	x		25	
Eucladium verticillatum	M	···	x	47	x	31
Fissidens coacervatus	M	yes	47		25	
Platyhypnidium riparoides	M	···	x	51		23
Rhynchostegiella litorea	M	···	27	54		
Rhynchotegiella teneriffae	M	yes	27			
Rhynchotegiella trichophylla	M	yes	36			
Sciuro-hypnum plumosum	M			47		
Tortella nitida	M	···	x		31	
Tortula solmsii	M	···	x		35	
Open stands						
Asterella africana	L	···	33		x	
Marchantia polymorpha	L	yes	39		38	x
Bryum argenteum	M		x	43		35
Bryum torquescens	M	···	x	37	38	43
Didymodon vinealis	M			39		x
Eucladium verticillatum	M	···	33		27	x
Fissides bryoides	M	···			x	33
Ptychostomum capillare	M	···	47	37	27	x
Trichostomum brachydontium	M	···	33	x	x	41

Notes: The four species with highest indicator values (ISA value) for each successional stage in the four combinations of substrate and environment are included (at $P < 0.05$, Monte Carlo test). In some environments (e.g., rocks in DW–WF), there are more than four species because at least two distinctive species had the same ISA value. The additional presence of a species is indicated by an "x." Abbreviations are: L, liverwort; M, moss; DW, dripping wall; ST, stream; WF, waterfall.

† Red-list condition according to J. M. González-Mancebo and A. Fernández-López (*unpublished manuscript*), considering the categories of endangered and vulnerable.

in disturbance effects across complex forest landscapes at various spatial and temporal scales (Lindenmayer et al. 2006, Pressey et al. 2007, Dynesius et al. 2009).

Responses to forest clear-cutting depending on habitat

We propose that the wetter substrates and the generally lower development of emergent ruderal vascular plant communities associated with dripping walls and waterfalls compared to streams (Table 1) might explain the larger differences between ancient forests and disturbed stages in streamside sites. The moisture below the dripping walls and waterfalls may buffer against changes in air microclimate (Hylander et al. 2005), whereas the higher cover of grasses (e.g., nitrophilous herbs) and shrubs (e.g., *Rubus ulmifolius*, *Arundo donax*) and, consequently, higher litter deposition might outcompete bryophyte species that typified undisturbed forested environments (González-Mancebo et al. 2004). Therefore, pre- vs. post-disturbance conditions would be more similar in the two former environments than in streams. In line with this, bryophyte communities on north-facing slopes (generally darker, moister, and colder and hence more similar to forested stands) of boreal forests were less affected by forest clear-cutting than those on south-facing slopes (Åström et al. 2007).

Nevertheless, we found a set of species exclusive to open streamside sites (Table 3, Fig. 4), indicating that competitive exclusion by vascular plants could not be the only cause of the differences in species composition along streams (Table 4). The stronger seasonal variation of the water level mirrored by a smaller area of permanently wet ground in the stream sites (Table 1) could probably contribute to the fact that such habitats

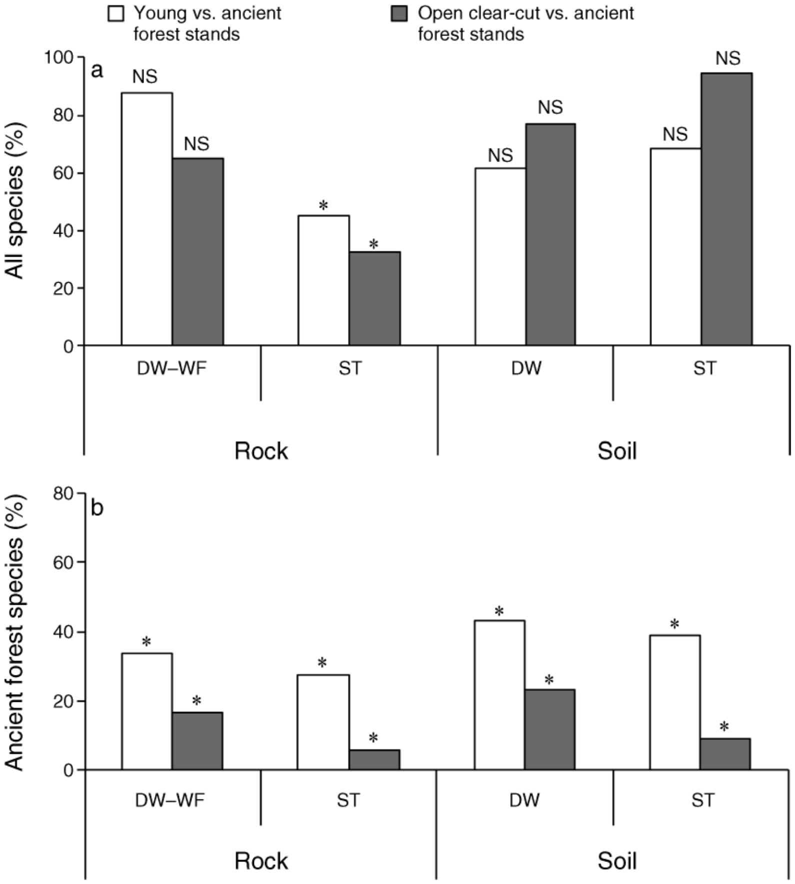

FIG. 3. Percentage of bryophyte species (i.e., pooled species numbers from the three systematic and the three subjectively chosen [1-m^2] subplots in each 0.01-ha plot) in young forests ($n = 16$) and open clear-cut stands ($n = 16$) relative to ancient forest stands ($n = 24$). The comparison was made in each combination of environment and substrate separately for (a) all species in each successional forest stage and (b) only "ancient forest species" (i.e., with significant higher indicator values [at $P < 0.05$] in ancient forests than in the other two successional stages). An asterisk above the bar indicates a significant ($P < 0.05$) difference between the young forests or the open stands and the ancient stands, respectively (Mann-Whitney U test; NS indicates nonsignificant difference). Abbreviations are: DW, dripping walls; ST, streams; WF, waterfalls.

were drier post-harvest environments for bryophytes. Under such stressful conditions, open clear-cut stands along streamside sites could be colonized by a set of drought-tolerant, early-successional bryophytes, most bioclimatically nonrestricted species such as *Ptychostomum capillare*, *Bryum* spp., *Didymodon vinealis*, *Trichostomum brachydontium*, and *Fissidens bryoides* (Table 3). The window of occurrence of many of these taxa (mostly mosses) in stream sites was, however, relatively short, as shown by the significant changes in species composition (Tables 2 and 3) that happened between open (~5–15 years) and young forest stages (~20–50 years). Thus, the young forest stands along streams were mainly characterized by *Eucladium verticillatum*, *Rhynchostegiella litorea*, and *Platyhypnidium riparioides* and by humid belt taxa such as *Asterella africana* (Table 3). The short-term duration of disturbance-favored taxa was also shown after clear-cutting of streamside boreal forests (Dynesius and Hylander 2007).

Responses to forest clear-cutting depending on substrate

The change in species numbers of most bryophyte groups tended to be larger for species growing on rock than for soil-growing species (Fig. 4). The small differences found for the number of bryophyte species on soils could indicate a higher capacity to resist post-harvest conditions, which is also indicated by the slightly higher proportion of ancient soil species than ancient rock species found in young and open stands (Fig. 3b). However, there were significant shifts in species composition after disturbance in (mainly) open clear-cut stands of dripping walls and streams (Table 2), supporting the suggestion that a guild of disturbance-tolerant soil bryophytes replaced a subset of ancient (laurel) forest species in stands without canopy cover (Table 3). Our findings corroborate several studies that have found rapid invasion by early-successional mosses and herbs on mineral soils subjected to clear-cutting (Elliott et al. 1997, Fenton et al. 2003, Hylander et al. 2005). One possible explanation might be that soil diaspore banks were activated under post-harvest conditions. Some studies have demonstrated high presence of bryophyte propagules in buried banks that usually only germinate following disturbance events and operate over short periods (Jonsson 1993, Ross-Davies and Frego 2004). Another possibility could be that human-induced disturbances created suitable conditions for the establishment of airborne propagules. Many early-successional species (i.e., colonists) tend to produce large amounts of small spores ($<$20 µm) that are easily dispersed by wind (During 1992, Hutsemekers et al. 2008). However, to understand the contribution of both propagule sources in community reassembly after anthropogenic disturbances, future studies on both fine- and landscape-scale patterns of diaspore distribution are necessary (Ross-Davies and Frego 2004, Frego 2007).

As mentioned previously, a higher number of species groups on rocks showed a negative response to forest clear-cutting. This was especially noteworthy in streamside sites, where even highly resilient bryophyte groups (e.g., mosses; Dynesius and Hylander 2007) had a lower number of species when rocks in disturbed sites are compared with ancient forest stands (Figs. 3 and 4). The lower persistence of bryophytes inhabiting rocks than soils (Fig. 3b) may be partly explained by the general shape and location of both substrates in the study system. Whereas rocks are convex substrates more exposed to drought conditions after clear-cutting (Hylander et al. 2005), soils could be associated with more concave forms, appearing often in more sheltered and subsequently moister microsites. Although many studies have recognized the buffering role of running water in cleared stands (Brosofske et al. 1997, Dynesius and Hylander 2007), our study supports the pattern of high susceptibility to local extinction of species on convex substrates (i.e., rocks) after clear-cutting (Hylander et al. 2005, Dynesius et al. 2009), also in subtropical riparian systems subjected to fog influence.

Most Canarian laurel forest areas are characterized by strong fog incidence, especially at altitudes ranging from 700 to 1100 m above sea level (Marzol 2008). Since altitude is a key factor affecting distribution of bryophyte assemblages on the forest floor (González-Mancebo et al. 2004), differences observed among sites might be considered an artifact of the study system and related to the fact that ancient forests were located at higher altitudes (strongest mist level) than young forest-open stands. However, even if our results show that altitude is an important variable in structuring communities, the somewhat skewed distribution of site types along the elevational gradient did not account for the differences among lotic environment types and the strong effects of disturbance on the bryophyte communities (Table 4).

Table 4. Analysis of covariance (ANCOVA) of the effect of the successional forest stage and freshwater habitat on total number of species in each site for each phylogenetic group for each type of substrate.

Variable	df	Liverworts *F*	Liverworts *P*	Mosses *F*	Mosses *P*
Rocks					
Main effects					
Freshwater habitat	2, 56	9.3	**<0.001**	6.9	**0.009**
Successional stage	2, 56	7.2	**0.003**	3.9	0.057
Covariates					
Altitude	1, 56	26.7	**<0.001**	36.9	**<0.001**
pH	1, 56		NS		NS
Cover of grasses	1, 56	11.6	**0.003**		NS
Permanently wet ground	1, 56	15.7	**<0.001**	7.9	**0.007**
Soils					
Main effects					
Freshwater habitat	1, 40	0.3	0.550	0.5	0.468
Successional stage	2, 40	1.3	0.270	0.5	0.583
Covariates					
Altitude	1, 40	8.2	**0.007**	4.7	**0.037**
pH	1, 40		NS		NS
Cover of grasses	1, 40	13.5	**0.001**		NS
Permanently wet ground	1, 40	9.6	**0.004**		NS

Notes: Freshwater habitat and successional forest stage were used as fixed factors, and altitude (m above sea level), pH, cover of grasses (%), and permanently wet ground (%) as covariates. Significant differences at $P < 0.05$ appear in boldface, and nonsignificant covariables are indicated (NS).

Responses to forest clear-cutting by bryophyte group

The results that liverworts showed a more negative response to the disturbances (Fig. 2, Appendix B) match with previous studies that found liverworts to be more sensitive than mosses to human-induced loss of forested habitats (Fenton et al. 2003, Hylander et al. 2005). Leafy liverworts are a very sensitive group to drought conditions due to their life-form traits (During 1992). However, we also found that some thallose liverworts were more frequent in ancient forest stands, such as *Dumortiera hirsuta* and *Aneura pinguis* (Appendix B). In contrast, particular species with recognized affinity to anthropogenic environments, such as *Marchantia polymorpha* (Stevenson and Hill 2008), were more related to disturbed forest and open clear-cut stages.

Red-listed species restricted to the laurel forest (e.g., *Acanthocoleus aberrans*, *Homalia webbiana*, *Tetrastichium fontanum*, and *Thamnobryum alopecurum*) were only found in undisturbed forested landscapes, hence showing high vulnerability to forest clear-cutting (Table 3; Appendix B). The two key substrates (rock and soil) were equally available in each environment along the successional gradient (Table 1), thus the pattern observed here seems to be related to the existence of stressful microclimatic conditions in both disturbed stages rather than to substrate availability. Our results hence support the notion that such species should be

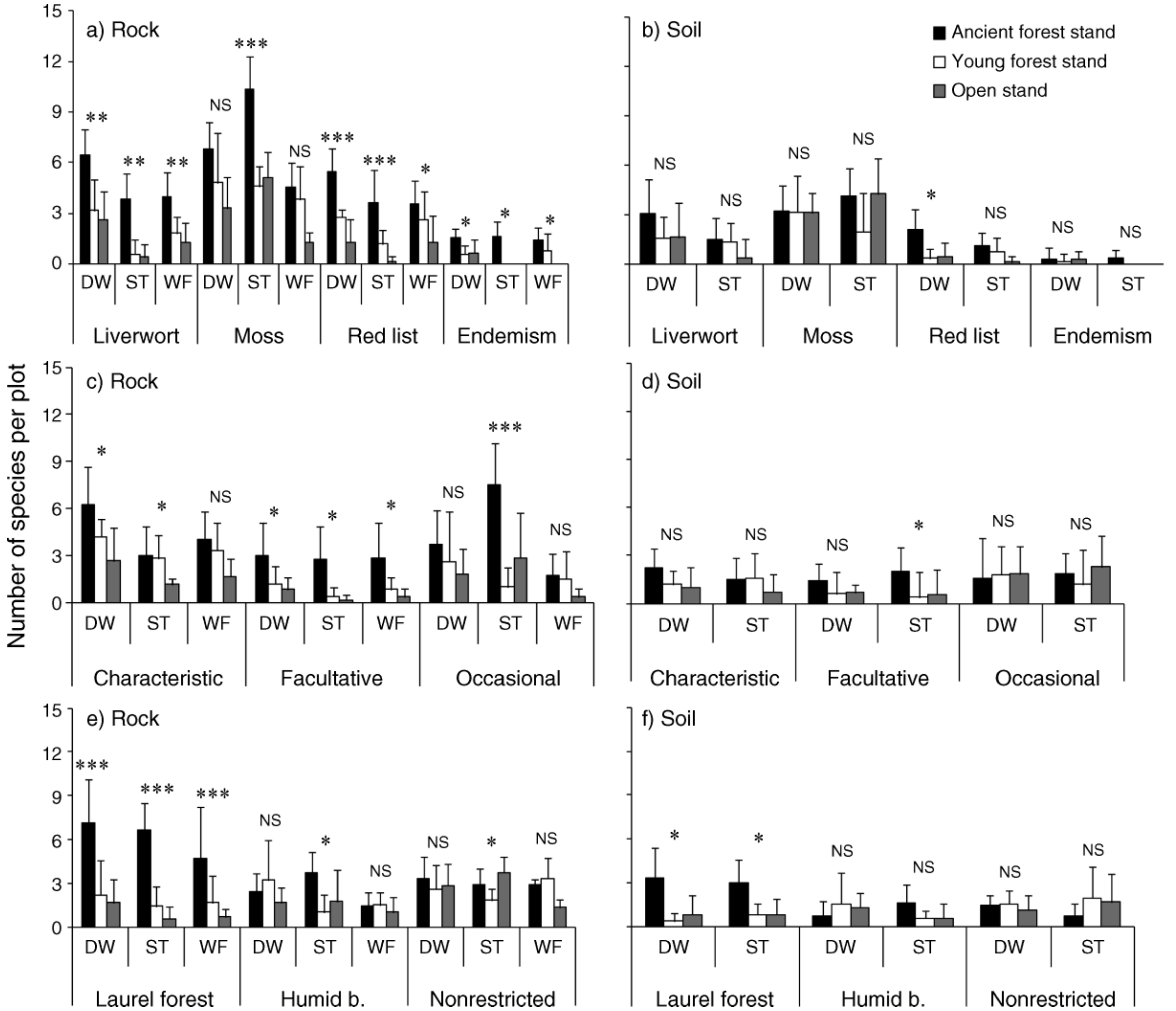

FIG. 4. Species richness (i.e., the number of species at the subplot [1-m^2] level using the three systematic subplots; mean + SD) in the three successional forest stages. The comparisons were made separately for dripping walls (DW), streamsides (ST), and waterfalls (WF); for (a, c, e) rocks and (b, d, f) soils; and for species groups based on (a, b) phylogenetic, red-listed, and endemic condition, (c, d) the affinity to the freshwater system, and (e, f) the affinity to the bioclimatic belt (Humid b., humid bioclimatic belt). Asterisks indicate groups of bars in which richness differs significantly between the three successional forest stages (Kruskal-Wallis test; NS indicates $P > 0.05$).

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

considered sensitive (J. M. González-Mancebo and A. Fernández-López, *unpublished manuscript*) and deserve inclusion in conservation lists and management plans.

Endemic species were both negatively and positively affected by forest clear-cutting (Fig. 2; Appendix B). This might be related to the fact that most endemics are typical for the laurel forest, whereas others, such as *Fissidens coacervatus*, naturally grow in more termophilous conditions at lower altitudes or are forest floor species that can survive outside the forest in freshwater environments (e.g., *Rhynchostegiella trichophylla*). A variable response to habitat modification was also found when the species were classified according to their affinity to freshwater systems (Fig. 2). For characteristic taxa, there might be certain species that are often submerged and, therefore, are less affected by drier conditions of clear-cut stands (Hylander et al. 2005, Dynesius et al. 2009). Facultative and occasional species also seemed to display noncongruent responses to forest clear-cutting; thus, other features such as phylogeny or ecological conditions in their principal distribution spots are likely more important.

To sum up, our findings indicate that most guilds of bryophytes are sensitive to human-induced habitat modifications and were not able to persist or reestablish stable populations in riparian habitats affected by disturbance events. Streamsides seemed particularly vulnerable. This result matches with the long periods of time usually needed by disturbance-intolerant species of vascular plants, macroinvertebrates, and bryophytes to recolonize after local extinction episodes caused by human degradation of forested riparian systems (Elliott

PLATE 1. Ancient cloud (laurel) forest stand at El Cedro, La Gomera Island, Canary Islands, Spain. Canarian riparian laurel forests play an essential role in the insular hydrological cycle and support unique species-rich aquatic and terrestrial ecological communities, including bryophytes. Given that the bulk of riparian forest environments across laurel forest landscapes have already been degraded by anthropogenic disturbances, the long-term conservation of their biodiversity might need active management to reestablish original conditions. Photo credit: A. B. Fernández-López.

et al. 1997, Dynesius and Hylander 2007, Lorion and Kennedy 2009).

Management and research implications

Given that the bulk of lotic environments across Macaronesian laurel forest landscapes have already been degraded by anthropogenic disturbances, with <10% being conserved in some islands (Malmqvist et al. 1995, Hughes and Malmqvist 2005), the long-term conservation of their biodiversity might need active management to reestablish original conditions. Thus, if threats such as agriculture or timber harvest are decreasing due to depopulation of rural areas (as is happening in the Canary Islands), we suggest that valuable opportunities might emerge to restore actively lotic environments across disturbed watersheds (Pressey et al. 2007).

The restoration of riparian forest patches within degraded catchments might imply major benefits, such as the creation of diversified habitats for vulnerable terrestrial and aquatic organisms or establishment of corridors for plant and animal dispersal (Naiman et al. 1993, Lindenmayer and Franklin 2002, Lindenmayer et al. 2006). If the recovery of lotic habitats and protection of their biota, including bryophytes, are one of the priority conservation targets (Malmqvist and Rundle 2002), landscape-level management planning should take special care of small streams with an abundance of rocks (Hylander et al. 2005). An additional possible management action might be the elimination of highly competitive shrubs or grasses (e.g., *Rubus ulmifolius*, *Arundo donax*, *Tradeschantia fluminensis*) in disturbed streamsides and, subsequently, reintroduction of natural riparian vegetation.

As the three freshwater environments included many vulnerable species, management efforts should not concentrate solely on stream environments. Indeed, the higher persistence of bryophyte communities on dripping walls and waterfalls does not mean that forestry activities such as clear-cutting do not impact their biota. Conversely, our results show that waterfalls and especially dripping walls may hold many of the bryophyte species that are greatly sensitive to clear-cutting and (even) some of these species could not be found in young forest stands, 20–50 years after disturbance. Management strategies deduced from our study might be sufficiently general to be applied to other subtropical insular regions. However, what constitutes a suitable habitat varies depending on species, communities, and local environmental conditions (Lindenmayer and Franklin 2002, Lindenmayer et al. 2006). Therefore, it is recommended that land managers adapt management measures to each insular region. We conclude that the impact of anthropogenic activities on insular communities deserves further careful attention since the risk of extinction due to human-induced habitat loss or modification may be exacerbated in isolated oceanic islands with relatively small total habitat area for focal organisms (Brooks et al. 2002, Whittaker and Fernández-Palacios 2007, Gillespie et al. 2008).

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APPENDIX A

A map showing the location of the 56 sites studied on La Gomera Island, Canary Islands, Spain (*Ecological Archives* A020-061-A1).

APPENDIX B

Species list including information on their phylogenetic group, red-list category, affinity to the freshwater habitat and the bioclimatic belt, and their indicator-species values (*Ecological Archives* A020-061-A2).

APPENDIX C

Spearman's correlation coefficients among habitat properties in the 56 freshwater sites analyzed (*Ecological Archives* A020-061-A3).