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Altitudinal distribution patterns of bryophytes in the Canary Islands and vulnerability to climate change☆

Francisco Lloret[a,*], Juana María González-Mancebo[b]

[a] Centre de Recerca Ecològica i Aplicacions Forestals (CREAF) and Unitat d'Ecologia, Departament de Biologia Animal, Biologia Vegetal i Ecologia, Universitat Autònoma Barcelona, Spain
[b] Departamento de Biología Vegetal (Botánica), Universidad de La Laguna, Tenerife, Islas Canarias, Spain

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ABSTRACT

We report the pattern of bryophyte distribution through the elevation gradient of three Canary Islands (Fuerteventura, Tenerife and Gomera) assessing their vulnerability risk to climate change. We considered a conservative scenario of upslope climatic shift of 200–400 m and a drop in the upper limit of the cloud belt from 1500 to 1000 m. Climate change vulnerability was analyzed from the overlap between the predicted shift in isotherms or cloud-belt edges and the current species range, following the Colwell and colleagues's model.

Liverworts show narrower ranges and tend to live at lower elevations than mosses. Perennials and long-lived shuttle species establish in the upper localities. Many perennials and most of the long-lived shuttle species grow in cloud forests. Many annual shuttle species and colonists establish in the lowest localities. Colonists also occupy the harsh summit in the highest islands.

In accordance with the Colwell model, most elements of this bryoflora appears vulnerable to rapid climatic change. Upland extinction and contraction challenges the bryoflora on the driest, lowest island Fuerteventura; range-shift gaps do this on the highest island Tenerife. Liverworts tend to be more vulnerable to range-shift gaps; mosses are more vulnerable to upland extinction. On the lowest island, perennials and long-lived shuttle species are more vulnerable to upland extinction; perennials are also vulnerable to range-shift gaps. Colonists are most vulnerable to upland contraction or extinction on the high islands Gomera and Tenerife. Annual shuttle species tend to be more vulnerable to lowland attrition on these high, most humid islands. Many elements of the bryoflora of the upper limit of the cloud forests appear to be vulnerable, while most of the flora of other cloud forest areas presumably will not be so affected, with the exception of the most restricted species.

A simple model illustrates the feasibility of preliminary assessments of climate change on organisms which show a lack of published detailed information on their distribution and biology. This assessment gains by incorporating estimates of biological attributes.

Introduction

Altitudinal gradients provide a classical framework to study the relationship between species distribution and climate because great climatic variation occurs within short geographical distances. This relationship is expected to be closer on islands, where limited dispersal reduces the occurrence of transient species (MacArthur and Wilson, 1967). The conditions of isolation may be intensified by the fact that climate on islands usually displays a strong oceanic influence and quite often proves to be anomalous with the respective latitude (Leuschner, 1996; Whittaker and Fernández-Palacios, 2007). The current global climatic change is likely to have a significant influence on species distribution on islands (Kazakis et al., 2007; Petit, 2008).

Recent studies support the notion that global warming is driving species ranges toward higher elevations (Engler et al., 2009; Kelly and Goulden, 2008; Lenoir et al., 2008). Successive field-observation surveys provide the definitive evidence of distribution shifts, but some degree of anticipation may be obtained by projecting future scenarios on to the current distribution of species. This approach is being used extensively for regional assessments on continents (Randin et al., 2009; Thuiller et al., 2005), but it is much less common for the analysis of elevation gradients on islands.

☆ *Nomenclature source:* González-Mancebo et al. (2008a, 2009b).
* Corresponding author at: Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Campus Universitat Autònoma Barcelona, 08193 Bellaterra, Barcelona, Spain.
E-mail address: Francisco.Lloret@uab.cat (F. Lloret).

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Recently, Colwell et al. (2008) proposed a simple model to illustrate the potential for altitudinal range shifts in the tropics when the full geographical ranges of species and the corresponding environmental variables are not always available to accurately model future distributions. In the model the current elevational range size is plotted as a function of the elevational midpoint and is compared to the predicted shift in isotherms. The model thus allows detecting those species without any overlap with the predicted ranges (Fig. 1). Initially considered as critical in tropical altitudinal gradients, all the vulnerability situations proposed in the model are also exacerbated on oceanic islands on account of the obstacles to immigration.

The impact of climate change on different biological groups will be determined by their sensitivity to the new conditions and the ability to adjust the distribution range. Bryophytes are found from the tropics to the polar regions, from sea level to mountain summits; thus they are good candidates for latitudinal and altitudinal studies (Andrew et al., 2003). Their diversity and abundance strongly reflect water availability, due to their poikilohydric nature, but they have also been reported to be highly sensitive to hot temperature (e.g., Dilks and Proctor, 1975). They are thus likely to be threatened by climate changes involving higher water deficit associated with increasing temperatures, more frequent climatic extremes (IPCC, 2007; Timmermann et al., 1999), or reduced cloud water in tropical mountain forests (Still et al., 1999). In fact, there are also important ecological differences between the two main phylogenetic groups within bryophytes: liverworts are in general more closely linked to moist habitats than mosses.

Several life-strategy types have been distinguished among bryophytes according to their lifespan, persistence under unfavourable conditions and dispersal ability (During, 1979, 1992). These traits are also related to growth form and characterize the bryoflora of microhabitats since these types represent differences in tolerance to drought and climatic disturbance (González-Mancebo and Hernández-Garcia, 1996; Kürschner et al., 1999; Lloret, 1988). Thus, the ecological significance of species distribution patterns may gain from merging individual patterns into these biologically based groups, which reflects ecological constraints (functional groups, *sensu lato*, or specific response groups, after Lavorel et al., 1997). Furthermore, variations in the vulnerability to climate change are to be expected between these groups. The analysis of climate change effects in this important group of plants is relatively scarce and often restricted to epiphytes (Lugo and Scatena, 1992; Zotz and Bader, 2009) and peat bog species (Gignac et al., 1998; Robroek et al., 2007; Whinam and Copson, 2006).

The Macaronesian Region includes a string of North Atlantic islands characterized by high rates of endemism in a vast array of organisms (Juan et al., 2000). Macaronesia is therefore one of the world's 25 hotspots of biodiversity and one of the most important floristic areas in terms of conservation within the European-Mediterranean climate region (Médail and Quézel, 1997). A relevant feature of the volcanic Canaries is the variability of their maximal elevation, ranging from 670 m in Lanzarote to 3717 m in Tenerife. This elevation gradient determines a permanent cloud belt in the otherwise semi-arid climate of the Canary Islands (Höllermann, 1981; Marzol, 2002). The cloud belt determines the existence of humid Tertiary relict forests that exhibit exceptional species richness, including bryophytes, restricted to this ecosystem (González-Mancebo et al., 2009c). These areas thus constitute one of the most species-rich regions within the European political territories (Fernández-Palacios et al., 2001). The Canaries might be particularly sensitive to climatic change on account of their small but highly diverse territory and the geographical location (IPCC, 2001). Sperling et al. (2004) assessed changes in the distribution of the laurel cloud forests of Tenerife according to dif-

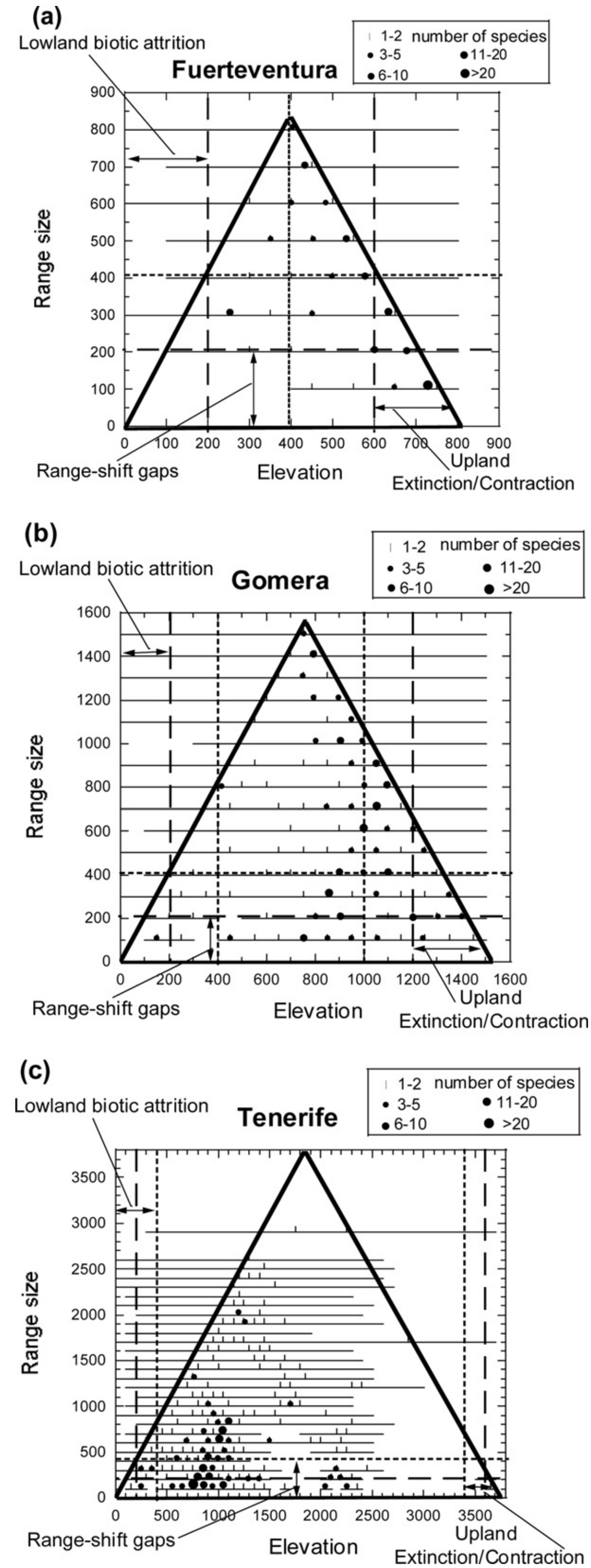

Fig. 1. Graphical model of the potential effects of climate warming on the distribution of species ranges on the three islands: (a) Fuerteventura, (b) Gomera, and (c) Tenerife. The elevational range size for each species (vertical axis) is plotted as a function of its elevational midpoint (horizontal axis), with corresponding range limits indicated by the solid horizontal lines. An upslope shift in isotherms with 1 °C and 2 °C warming climate increase is illustrated, respectively, by dashed and dotted horizontal and vertical lines. Lowland biotic attrition: if lowland ranges shift upslope, their new lower range limits must lie at or above the vertical lines. Range-shift gaps: if elevational ranges follow isotherms upslope, no projected range smaller than the

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ferent climatic scenarios. Their model suggests a downward shift in the area climatically suitable for laurel forests. Nevertheless, evidence on effects of climate change on the Macaronesian mountain flora is still scarce (Petit, 2008; Sperling et al., 2004).

In the present study we analyzed the relationship between bryophyte distribution and altitude as a likely proxy for climate, notably temperature, on three different isles in the Canaries, according to the location of the humid mountain bioclimatic belt (Tenerife, Gomera and Fuerteventura). Vulnerability to climatic scenarios was analyzed by following the four processes described by Colwell et al. (2008), considering total species richness and grouping species according to their broad phylogenetic affinity (mosses and liverworts) and their life strategy (annual shuttle species, colonists, long-lived shuttle species and perennials, following During, 1979, 1992). Our hypotheses were:

- The distribution pattern in the elevation gradient of the group that is most dependent on permanently humid microhabitats (i.e. liverworts) is associated with the cloud belt and exhibits narrower ranges.
- The distribution pattern of species with different life-histories along the elevational gradient responds to changes in the temporary suitability of the environment to bryophytes.
- The importance of the different types of vulnerability depends on the characteristics of the islands: upland extinction and contraction would be more significant on islands with lower elevation, while range-shift gaps would be more prominent on islands with a long elevation gradient.
- The vulnerability to climate change of the different groups will reflect their distribution patterns and will vary between islands with different elevations.

Study area

The Canary Islands constitute a volcanic archipelago located in the eastern subtropical north Atlantic, off the hyper-arid coast of Northwest Africa. The islands are characterized by outstanding biodiversity, featuring high levels of endemism, and spectacular radiations.

The mountains on these islands act as topographical barriers to humid trade winds, which are forced to ascend, thereby establishing a strong topoclimatic gradient with a strong differentiation between the windward and leeward sides of the islands (Fernández-Palacios and de Nicolás, 1995). Specifically, orographically induced adiabatic cooling leads to the daily development of a cloud belt on the windward slope of the island during the dry summer months. Clouds therefore develop from 750 m and trade wind inversion determines the upper limit of the cloud belt at around 1500 m a.s.l. (Sperling et al., 2004). Thus, the altitudinal gradient displays major ecosystem types from semi-arid scrublands, through sub-tropical broad-leaved evergreen and xeric endemic pine forests to high-altitude sub-alpine and alpine formations (Fernández-Palacios and Whittaker, 2008).

The selected islands, Fuerteventura, Gomera and Tenerife, rise to an altitude of 807 m, 1484 m and 3717 m, respectively. Fuerteventura is the most arid island due to its proximity to the Saharan coast (98 km) and the fact that its maximum altitude coincides with the lowest limit of the humid trade wind. Moreover, the introduction of herbivorous species has produced a great impoverishment in all plant groups, including bryophytes (González-Mancebo et al., 2009a). The opposite situation occurs in Gomera, where the richest ecosystem, the evergreen cloud forest, is situated in the upper area of the island (from 700 m) and is well preserved. Thus, Gomera has higher bryophyte richness than expected for its area (294 species in 368 km^2: González-Mancebo et al., 2008a). Finally, Tenerife has the greatest richness of bryophytes (416 species), mainly due to its highest altitude (González-Mancebo et al., 2008a) and the marked differences between its windward and leeward slopes. Accordingly, the evergreen cloud forests (laurel forest and *Erica-Myrica* woodlands) grow in the northern part of the island from 700 m to 1200 m (occasionally up to 1500 m). Drought-tolerant species on windward slopes therefore often present discontinuous distribution below and above the cloud belt.

Materials and methods

Climatic scenarios

In the Canaries the mean temperature varies from 18 to 22 °C in the lowest semi-desert area from 14 to 18 °C in the humid mountain forests, from 11 to 14 °C in the xeric pine forest and less than 11 °C in the sub-alpine and alpine belts (Del Arco et al., 2006, 2009). Rainfall values range from 150 to 300 mm in the driest area to 700 to 900 mm in the humid mountain belt (Marzol et al., 1990). The additional mist precipitation caused by the Northeast tradewinds, particularly in the summer months, ranges from 0–50 mm to more than 700 mm.

As in many other regions of the world, a shift to higher temperature conditions has been recorded in the last few decades (Petit, 2008; Sperling et al., 2004). Indeed, current climate models suggest an increase of 2.1 °C [from +1.9 to +2.4] in Macaronesia (IPCC, 2007; see also Sperling et al., 2004). On the basis of data from the Spanish Servicio Metereológico Nacional (INM), we estimate an average current decrease of 1 °C in mean annual temperature for every 200 m of upslope on Tenerife; we thus considered a conservative scenario of a likely upslope climatic shift of 200 and 400 m.

Climate change is also expected to modify the altitudinal distribution of the cloud belt that develops in the north part of Tenerife and on the top of Gomera. We applied the predictions of Sperling et al. (2004), who analyzed several climatic models and proposed that the upper limit of the cloud belt is likely to descend from 1500 to 1000 m in the next decades due to drier and sunnier conditions. Although trade winds also provide some degree of humidity on the peak of Fuerteventura, cloud forests do not develop there and we did not consider this island in the analysis of the effect of cloud-belt shift on bryophyte distribution.

Bryophyte data bank

Data for the species distribution ranges in the considered islands were obtained from the literature (mostly compiled by Losada-Lima et al., 2007), from herbaria information and from field surveys. All taxa were considered at specific levels, according to the latest compilations (González-Mancebo et al., 2008a, 2009b) – see Appendix.

Life-strategy categories were assessed following During (1979, 1992) and are detailed in the Appendix. We preferred this classification to other categories exclusively based on growth-form because it also includes dispersal attributes. We considered the four best represented categories in the Canaries: (a) annual shuttle species (hereafter, annuals) – with short-distance spore dispersal and short lifespan, usually a few months; (b) colonist – with spores capable for long-distance dispersal, and short lifespan, between 2 and 5 years, including pioneer and gap-dependant species; (c) long-lived

Fig. 1. horizontal lines will overlap its prewarming elevational range, challenging migration. Range contraction and mountaintop extinction: all ranges with upper limits less than the vertical lines are predicted to contract, and those included between the lines and the summit face local extinction. Symbol size is proportional to the number of species with the same distribution.

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shuttle species–short-distance dispersal spore and lifespan of up to around 20 years; (d) perennial – with long-distance spore dispersal and very long lifespan. Less species belonged to other categories (i.e. fugitives, short-lived shuttle species) and they were not included in the analysis.

Data analysis

We considered four variables to describe the distribution pattern of bryophytes on the altitudinal gradient: highest and lowest elevation of occurrence, range (highest minus lowest elevation) and an index that estimates discontinuity (Discontinuity = greatest interval within the range without species occurrence/range). This discontinuity index is dependent on the elevation of the island (larger species distribution ranges are expected on higher islands), so it allows comparisons between species (or groups of species) on the same island but not between islands. For each island we analyzed by ANOVA the differences in the distribution pattern between mosses and liverworts (including hornworts), and those between the life-strategy categories. We used the four descriptors of the distribution pattern (highest and lowest elevation, range, discontinuity index) as dependent variables and the phylogenetic types (mosses and liverworts) and life-strategy types as fixed explicative factors. Since a number of species did not belong to any of the four considered life-strategy types, we increased the number of replicates for the mosses *vs* liverworts comparison by performing separate one-way ANOVAs for the phylogenetic and life-strategy types. No transformations were needed to attain the requirements of this test.

Vulnerability under future climatic scenarios was analyzed by considering the four processes described by Colwell et al. (2008), based on the assumption that the species range must shift upslope by a certain interval equivalent to the expected increase in temperature (Fig. 1). **Lowland biotic attrition** refers to sets of species with lowland ranges below the expected shift; in other words, their new lower range limits lie at or above their current range limit. Community vulnerability would arise in islands due to the absence of corridors allowing the immigration of species able to replace species restricted to lowlands. **Range-shift gaps** correspond to species with an elevation range smaller than the projected shift, i.e. without any overlap between the pre-warming and the projected range, which poses challenges to dispersal and establishment. In **upland contraction**, species showing ranges with upper limits above the projected climatic upper domain (i.e., with upper limits above the line defined by the current upper domain minus the projected range shift) are predicted to experience reductions in their range. Among these species, **upland extinction** will occur for those with a range smaller than the predicted range shift, i.e., with their lower limit also above the line defined by the current upper domain minus the projected range shift.

We calculated for each island the number and percentage of species belonging to the different taxonomic and life-strategy categories that were vulnerable according to these processes. Comparisons between species belonging to these categories were performed by χ^2 tests that considered scenarios of increases of 1 °C and 2 °C (200 m and 400 m upslope shifts, respectively). We also calculated the percentage of the total number of species that were vulnerable in scenarios of increases of up to 4 °C (800 m upslope shift).

Vulnerability to a shift in the distribution of the cloud belt was estimated for Gomera and Tenerife by selecting those species that currently live exclusively within the range of elevation where the cloud belt occurs (from 700 to 1500 m a.s.l.). This analysis could not be confined to the northern part of the islands because the information on species distribution was not sufficiently detailed. Vulnerability may therefore have been overestimated because some species found within this range can probably live outside the cloud belt. Since climatic predictions suggest a drop in the upper limit of the cloud belt to 1000 m a.s.l., we finally considered as vulnerable to upland attrition those species with a current lowest limit of distribution at or above 1000 m a.s.l.

Results

Altitudinal patterns of distribution

As hypothesized, liverworts show narrower ranges than mosses, especially on the two islands with enough altitudinal gradients to reflect this pattern, Gomera and Tenerife (Table 1). Examples are several species of *Calypogeia* (*C. fissa*, *C. sphagnicola*, *C. suecica*), *Diplophyllum albicans*, *Jubula hutchinsiae*, *Lejeunea* (*L. flava*, *L. mandonii*), *Marchesinia mackaii*, *Metzgeria* (*M. conjugata*, *M. leptoneura*, *M. temperata*), *Nardia* (*N. geoscyphus*, *N. scalaris*), *Radula* (*R. jonesii*, *R. wichurae*), *Colura calyptrifolia*, *Jungermannia gracillima*, *Lophozia bicrenata*, *Plagiochila* (*P. stricta*, *P. maderensis*, *P. punctata*). Liverworts and hornworts (for instance, *Anthoceros agrestis*, *Riccia trabutiana*, *Southbya nigrella*) tend to be found at lower elevations than mosses on the more humid Gomera (highest elevation mean) and Tenerife (lowest and highest elevation means). Mosses show more discontinuity in Gomera (e.g. *Barbula unguiculata*, *Crossidium crassinerve*, *Dialytrichia mucronata*, *Dicranella heteromalla*, *Fissidens ovatifolius*, *Gyroweisia reflexa*), while this is only marginally the case in Tenerife (*Fabronia pusilla*, *Pseudotaxiphyllum elegans*) and the distribution of liverworts is more discontinuous in Fuerteventura (*Cephaloziella stellulifera*, *Riccia atromarginata*).

Life-strategy categories present different altitudinal patterns. Perennials (such as the mosses *Andoa berthelotiana*, *Isothecium myosuroides*, *Leptodon smithii*, *Neckera complanata*, *Pterogonium gracile* and the liverworts *Marchesinia mackaii*, *Plagiochila virginica*, *Plagiochila bifaria*) and long-lived shuttle species (for instance, the moss *Leucodon canariensis*, and the liverwort *Frullania teneriffae*) are more prone to establishing themselves on the upper part of the gradient on the most arid island (Fuerteventura), where they also show a narrower range than annuals and colonists. On Gomera and Tenerife, many perennials and long-lived shuttle species are found in the cloud forests, with a fairly continuous distribution and narrow range. Some typical examples of these species are *Isothecium myosuroides*, *Leucodon canariensis*, *Leptodon longisetus*, *Leucodon canariensis*, *Neckera complanata*, *N. cephalonica*, *Pseudoscleropodium purum*, *Porella canariensis*.

Alternatively, annuals (for instance, *Riccia lamellosa*, *R. trabutiana*) and colonists (for instance, *Aloina ambigua*, *Funariella curviseta*, *Tortula canescens*) establish themselves more on the lowest part of the elevation gradients, especially on the driest island (Fuerteventura). This is also true of the annuals on Gomera and Tenerife (the mosses *Acaulon triquetrum*, *Entosthodon commutatus*, *E. pulchellus* and the liverworts *Riccia cavernosa* and *R. trabutiana*). On these two islands, annuals and colonists show a similar pattern of discontinuity, and they are more discontinuous than perennials and long-lived shuttle species. Finally, colonists (*Coscinodon cribrosus*, *Dicranella varia*, *Syntrichia fragilis*, *Schistidium apocarpum*, *Ptychostomum pallens*, *P. pallescens*, *P. pseudotriquetrum*) occupy mostly the upper part of the gradient in the highest island, Tenerife, where they occupy the largest altitudinal range.

Vulnerability to climate change

The percentage of bryoflora vulnerable to the considered climatic change in the elevation gradient is high (Table 2), achieving values of close to 80% in Fuerteventura for an 1 °C increase, equivalent to 200 m of climatic upward displacement). The vulnerability

Table 1
Mean (and SD) values of the variables describing the distribution pattern of bryophytes in the altitudinal gradient of the three islands. Bryophyte species are grouped according to two types of categories: taxonomic (mosses and liverworts) and life-strategy (annual shuttle -annual-, colonist, long-lived shuttle and perennial, following During, 1979) categories. Comparisons within these groups were performed by one-way ANOVA, followed by Fisher's PLSD post hoc tests. Different letters following mean values indicate significant differences.

	n	**Fuerteventura**							
		Lowest elevation		Highest elevation		Range		Discontinuity	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mosses	83	360a	243	716a	130	356a	222	0.017a	0.072
Liverworts	37	427a	213	732a	125	305a	178	0.048b	0.119
Annual	18	328a	224	706a	143	378a	186	0.030a	0.087
Colonist	70	321a	240	693a	141	371a	228	0.027a	0.097
Long-lived	9	511b	127	778ab	67	267ab	100	0.037a	0.111
Perennial	15	600b	107	800b	0	200b	107	0a	0
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Mosses *vs* Liverworts		2.11	0.148	0.43	0.514	1.49	0.224	3.21	0.076
Life strategy		8.20	<0.001	3.69	0.014	3.56	0.017	0.46	0.710

	n	**Gomera**							
		Lowest elevation		Highest elevation		Range		Discontinuity	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mosses	186	601a	360	1222a	307	620a	392	0.084a	0.171
Liverworts	98	600a	264	1117b	305	517b	339	0.035b	0.099
Annual	28	429a	293	993a	326	564a	326	0.136a	0.178
Colonist	143	596b	380	1210b	296	614a	424	0.090a	0.178
Long-lived	23	643b	246	1217b	333	535a	260	0.014b	0.070
Perennial	63	662b	190	1197b	267	535a	307	0.026b	0.090
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Mosses *vs* Liverworts		0.001	0.979	7.42	0.007	4.86	0.028	6.85	0.009
Life strategy		3.55	0.015	4.24	0.006	0.69	0.558	5.26	0.002

	n	**Tenerife**							
		Lowest elevation		Highest elevation		Range		Discontinuity	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mosses	271	800a	621	1620a	728	820a	725	0.119a	0.242
Liverworts	130	638b	377	1174b	505	535b	509	0.073a	0.238
Annual	44	509a	430	1141a	544	632ab	601	0.118ab	0.237
Colonist	208	808b	651	1600b	778	792b	748	0.121b	0.238
Long-lived	38	737ab	383	1268a	515	532a	421	0.027a	0.134
Perennial	74	709ab	253	1373a	501	664ab	537	0.072ab	0.214
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Mosses *vs* Liverworts		7.50	0.006	39.65	<0.001	16.18	<0.001	3.21	0.074
Life strategy		3.74	0.011	7.59	<0.001	2.26	0.081	2.44	0.064

of the bryoflora varies between the islands, according to their maximum altitude and climatic characteristics.

As expected, on the island with the lowest elevation and most arid climate (Fuerteventura), the greatest vulnerability is to upland extinction and contraction, while lowland attrition is not expected to have any great effect under an increase of 1 °C (Figs. 1 and 2). Given the short elevation gradient on this island, a 2 °C increase will only cause major problems for the relatively few species (8%) that are restricted to the lowest 400 m. The highest island (Tenerife) shows a quite different pattern, with very few species vulnerable to upland extinction and contraction because the harsh conditions of the upper altitudes currently restrict the presence of vegetation, including bryophytes. On this island, the greatest vulnerability is associated with range-shift gaps that could affect 30% of the bryoflora in the 1 °C increase scenario and 45% in the 2 °C increase scenario. Species vulnerable to lowland attrition are almost negligible on this island. Gomera exhibits an intermediate pattern, with a very significant vulnerability to upland contraction (55 and 70% of the bryoflora, 1 °C and 2 °C increase, respectively) and levels of vulnerability to range-shift gaps and lowland attrition similar to those of Tenerife.

In general, the vulnerability pattern of mosses and liverworts is quite similar. However, liverworts exhibited significantly higher vulnerability to range-shift gaps on Tenerife (2 °C increase, $\chi^2 = 6.99$, $P = 0.008$) and marginal vulnerability to lowland attrition on Gomera (1 °C increase, $\chi^2 = 2.94$, $P = 0.086$), while mosses were more vulnerable to upland extinction on Gomera (1 °C and 2 °C increase, $\chi^2 = 3.63$, $P = 0.057$ and $\chi^2 = 8.85$, $P = 0.003$, respectively).

There were also differences in the vulnerability of the life-strategy types, but these differences change from one island to the other. Perennials were significantly more sensitive to range-shift gaps than the other types on Fuerteventura (1 °C and 2 °C increase scenarios, $\chi^2 = 4.84$, $P = 0.028$, $\chi^2 = 9.62$, $P = 0.002$, respectively) but less so on Tenerife (1 °C increase scenario, $\chi^2 = 5.97$, $P = 0.015$). Perennials were also more sensitive to upland extinction on Fuerteventura (1° C increase, $\chi^2 = 8.08$ $P = 0.044$). Colonists are the most vulnerable to upland contraction on Tenerife, the island with an alpine summit (1 °C and 2 °C increase, $\chi^2 = 3.45$, $P = 0.020$, $\chi^2 = 41.99$, $P < 0.001$, respectively) and to upland extinction on Gomera (2 °C increase, $\chi^2 = 9.93$, $P = 0.002$). Finally, in the case of annuals the number of sensitive species is low but they seem to be more vulnerable to lowland attrition on Gomera (2 °C

Table 2
Climate change vulnerability of bryophyte species from three Canary Islands. Several processes associated to species migration in mountain regions are considered: lowland attrition, range-shift gaps, upland extinction and contraction. Values correspond to the percentage of vulnerable species belonging to different taxonomic (mosses and liverworts) or life-strategy (annual shuttle -annual-, colonist, long-lived shuttle and perennial, following During, 1979) categories. Two climatic scenarios are considered: 1 °C and 2 °C increase of mean annual temperature corresponding to around 200 m and 400 m upwards shift, respectively.

Fuerteventura	*n*	200 m (1 °C)				400 m (2 °C)			
% Species		Lowland attrition	Range-shift gaps	Upland extinction	Upland contraction	Lowland attrition	Range-shift gaps	Upland extinction	Upland contraction
Total	125	0	37.6	28.0	79.2	8.0	74.4	54.4	92.0
Mosses	88	0	37.5	27.3	79.5	9.1	67.1	52.3	90.9
Liverworts	37	0	37.8	29.8	78.4	5.4	78.4	59.5	94.6
Annual	18	0	27.8	22.2	72.2	11.1	61.1	38.9	88.9
Colonist	70	0	35.7	22.9	72.9	11.4	62.9	42.9	88.6
Long-lived	9	0	0	22.2	88.9	0	22.2	88.9	100
Perennial	15	0	60.0	60.0	100	0	100	100	100

Gomera	*n*	200 m (1 °C)				400 m (2 °C)			
% Species		Lowland attrition	Range-shift gaps	Upland extinction	Upland contraction	Lowland attrition	Range-shift gaps	Upland extinction	Upland contraction
Total	284	1.41	23.6	5.6	55.6	3.9	43.3	13.4	70.4
Mosses	186	0.5	22.6	7.5	62.4	2.7	39.2	17.7	76.3
Liverworts	98	3.1	24.5	2.0	43.9	4.1	49.0	5.1	60.2
Annual	28	3.6	25.0	0	39.3	10.7	39.3	3.6	50.0
Colonist	139	1.4	25.2	7.2	57.6	2.2	43.2	18.7	74.8
Long-lived	23	0	13.0	8.7	65.2	4.3	34.8	8.7	69.6
Perennial	61	0	19.7	3.3	54.1	0	42.6	4.9	68.8

Tenerife	*n*	200 m (1 °C)				400 m (2 °C)			
% Species		Lowland attrition	Range-shift gaps	Upland extinction	Upland contraction	Lowland attrition	Range-shift gaps	Upland extinction	Upland contraction
Total	401	0.25	29.9	0.7	2.0	3.24	45.9	0.7	2.2
Mosses	271	0	27.3	0.7	2.2	4.06	41.3	0.7	2.6
Liverworts	130	0.77	32.3	0.8	1.5	1.54	55.4	0.8	1.5
Annual	44	2.3	36.4	0	0	9.09	50.0	0	0
Colonist	203	0	30.5	1.5	3.4	3.94	45.3	1.5	3.9
Long-lived	38	0	34.2	0	0	0	47.4	0	0
Perennial	72	0	19.4	0	0	0	44.4	0	0

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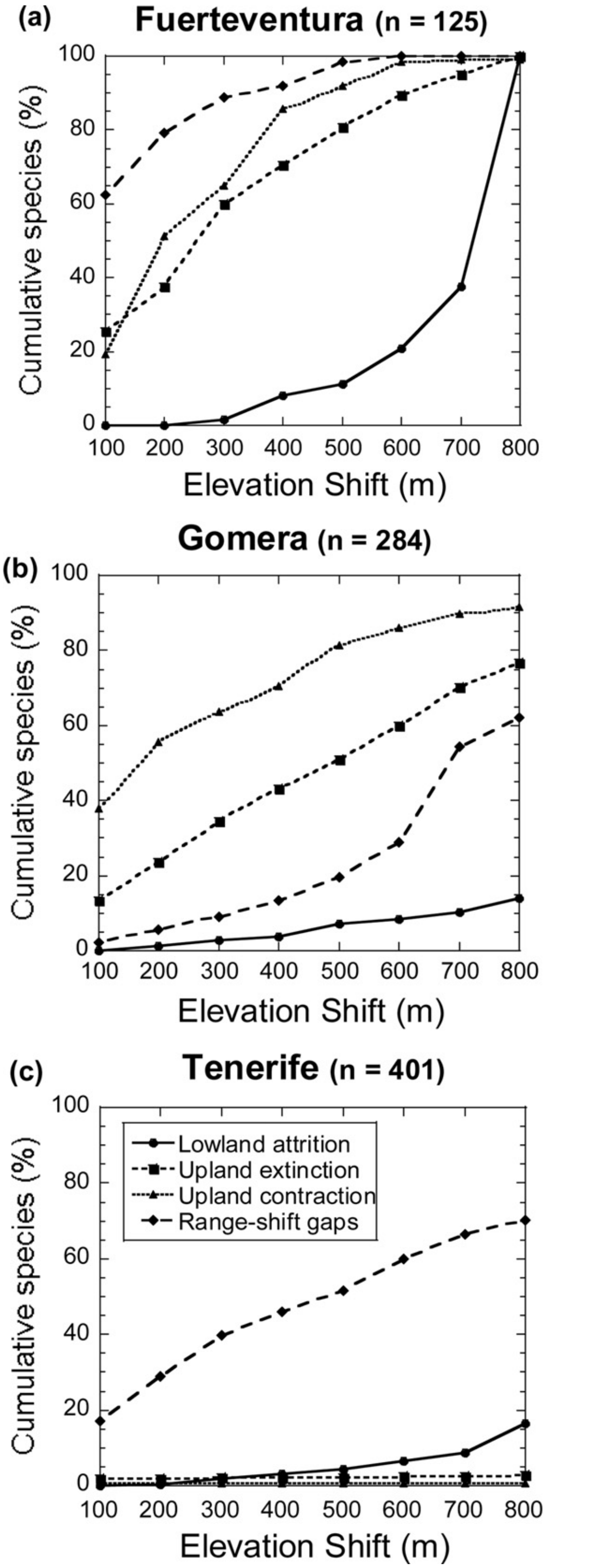

Fig. 2. Cumulative percentage of bryophyte species vulnerable to the four responses as a function of warming-driven elevation shifts on the three islands: (a) Fuerteventura, (b) Gomera, and (c) Tenerife. The *x* axis represents the elevation shift associated to increasing temperatures (1 °C equivals to 200 m). For each island, the total number of species (*n*) is given in the heading.

increase, $\chi^2 = 7.30$, $P = 0.007$) and Tenerife (1 °C and 2 °C increase, $\chi^2 = 7.13$, $P = 0.008$, $\chi^2 = 5.07$, $P = 0.024$, respectively).

The number of species exclusively living within the altitudinal range where the cloud belt occurs (700–1500 m a.s.l.) is remarkably high, accounting for around half the bryoflora of the two islands Gomera and Tenerife (Table 3), with liverworts tending to occupy these locations more than mosses, particularly on Tenerife. According to the life-strategy type, around 60% of perennials live exclusively in this range, followed by long-lived shuttle (50–55% of the species). Annuals are the group of species with the least exclusivity for this range. Due to its higher altitude and habitat heterogeneity on Tenerife, the percentage of the bryoflora exclusively living there in this range is somewhat smaller than on Gomera for all categories.

The analysis of upland attrition due to the shift of the cloud belt shows that a relevant proportion of the bryoflora (25% on Gomera and 17% on Tenerife) of these areas is vulnerable to the considered climatic conditions. However, there is an important variability between islands, and between taxonomic and life-strategy categories. Mosses are more vulnerable than liverworts on both islands (Table 3; Gomera, $\chi^2 = 12.08$, $P < 0.001$; Tenerife, $\chi^2 = 2.98$, $P = 0.084$). Colonists form the life-strategy group with by far the most vulnerable species on both islands (Gomera, $\chi^2 = 10.03$, $P = 0.002$; Tenerife, $\chi^2 = 6.96$, $P = 0.008$), although on Tenerife the percentage of annuals that are vulnerable is also rather high ($\chi^2 = 4.58$, $P = 0.032$). Among perennial species, only one (*Scleropodium cespitans*) proves to be vulnerable on Tenerife, while three (*Brachytheciastrum velutinum*, *Scorpidiurium circinatum*, *Sciuro-hypnum plumosum*) are vulnerable on Gomera. Finally, only two long-lived shuttle species (*Hedwigia ciliata*, *H. stellata*) were vulnerable on Gomera.

Discussion

The interpretation of the distribution patterns of Canarian bryophytes shows consistent patterns with even gain of interpretation details when considering life-strategy types: the environments with permanently suitable conditions (cloud forests) would mainly favour the growth of large, long-lifespan species, while in harsher environments with pulses of favourable conditions (for instance arid lowlands, alpine summits) species with short-lifespan and slow-growth will be more common. These patterns become clearer when the climatic and topographical context of each island is taken into account. Moreover, the differences between islands might also be explained by differences in microhabitat distribution, especially in the case of perennials. For instance, the high discontinuity values of perennials on Tenerife are probably related to specific water-rich refugee habitats as lava tunnels, that permit some laurel forest species to grow above 2000 m of elevation. On the driest island, perennials and long-lived shuttle species are confined to the more humid summits, where they become vulnerable to upland extinction, while annuals and colonists are more frequently found in lower, drier conditions. The affinity of annuals to more arid seasonal habitats is reinforced by their distribution at lower elevations on Gomera and Tenerife (for instance *Acaulon triquetrum*, several species of the genus *Riccia* and *Entosthodon*), while some species (e.g. *Riccia sorocarpa*, *Entosthodon muhlenbergii*) are also able to occupy arid areas on the summit of Tenerife. On the moister, higher islands (Gomera and Tenerife), the location of cloud-belt laurel forests determines the distribution pattern of life-strategy groups. Since most of the long-lived shuttle species and many perennials are confined to these habitats, they tend to have less discontinuity than annuals and colonists. In these two islands, long-lived shuttle species and perennials have similar ranges, being somewhat narrowest

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Table 3
Vulnerability (*n*, species number and percentage) to the altitudinal shift of the cloud belt in the two islands where it occurs. This shift corresponds to a descend from 1500 to 1000 m a.s.l. of the upper limit of the cloud belt. Only those species currently living between 700 and 1500 m have been considered (bryophyte flora in the cloud belt); from them, the number of species (*n*) and the percentage (%) for the different taxonomic (mosses and liverworts) and life-strategy (annual shuttle -annual-, colonist, long-lived shuttle and perennial, following During, 1979) groups are given.

	Gomera			Tenerife		
	Flora in the cloud belt (%)	Predicted attrition (*n*)	Predicted attrition (%)	Flora in the cloud belt (%)	Predicted attrition (*n*)	Predicted attrition (%)
Total	54.6	38	25.5	40.9	28	17.1
Mosses	52.7	33	33.7	34.3	20	21.5
Liverworts	58.2	5	8.8	54.6	8	11.3
Annual	25.0	1	14.3	36.4	6	37.5
Colonist	55.4	26	33.8	35.0	18	25.4
Long-lived	56.5	2	15.4	50.0	0	0
Perennial	62.3	3	7.9	58.3	1	2.4

on Tenerife. Long-lived shuttle species are characteristic epiphytes (During, 1979; Kürschner et al., 1999), which in the Canaries mainly occur on laurel forest trees (González-Mancebo et al., 2008b). This life-strategy has a narrower range than that of the perennials, a group with many more species able to grow outside the cloud forests (for instance, *Scleropodium touretii* or *Hypnum* spp.0, which occur on soils and as epiphytes in the drier pine forests, respectively).

Cloud forests also influence the distribution of liverworts and mosses. Many liverworts – mostly belonging to the order of Jungermanniales – are restricted to these forests (for instance, oceanic and endemic species of the genera *Radula* and *Plagiochila* – González-Mancebo et al., 2008b, 2009b,c). In addition, on the islands with cloud forests liverworts show narrower ranges, lower mean elevations and less discontinuity than mosses. This trend explains the higher vulnerability of liverworts to range shift gaps on Tenerife. Furthermore, the expected descend in the altitudinal range of cloud belts would produce more impact on mosses than on the liverwort flora, probably because liverworts tend to be distributed at lower elevations, in the areas directly affected by clouds during summer. However, since mosses are not restricted to cloud forests, a descend of the upper limit of the cloud level is not likely to produce dramatic effects on the bryoflora restricted to cloud forests.

The estimate of vulnerability is based on a rough forecast of the climate change effect on cloud forests (we even assumed that the shift on Gomera would be similar to that predicted for Tenerife by Sperling et al., 2004); so they must be considered with caution. In fact, the temperature changes are expected to promote an upward shift, while the cloud belt determining laurel forests would be shifting downwards. We analyzed both phenomena separately, but their combination may increase the species' difficulties in adjusting their distribution under the new conditions.

Above the cloud belt, there are also contrasted patterns between mosses and liverworts. On the highest island (Tenerife), the few species that are able to survive in the harsh conditions of the highest locations are mostly colonist mosses, making this group particularly vulnerable to upland extinction and contraction. On the more humid summits of Gomera, the proportion of mosses living in the uppermost locations is also high. We have not found any significant differences in the mean elevation and range of mosses and liverworts on Fuerteventura, probably due to the impoverishment occurring in the summit of this island. However, some dominant mosses (*Neckera intermedia*, *Leucodon canariensis*, *Cryptoleptodon longisetus*) characteristic of laurel forests have been found in the uppermost locations, suggesting the existence, until recently, of relict evergreen forests (González-Mancebo et al., 2009a) that have subsequently been destroyed by human action.

Adverse effects of climate change on bryophytes can be mitigated by the ability of these plants to retreat to suitable micro- or mesohabitats, which makes difficult assessments at a regional scale. Although the probability of occurrence of suitable microhabitats is also a function of mesoscale environmental conditions, the Canary Islands represent the overall southern or northern distribution limit for many species, even the western limit for some Mediterranean ones. In these cases, the possibilities to find suitable habitats for these naturally restricted populations is not as high, as in species located in the central areas of their distribution ranges. In fact, vulnerability, as considered in this paper, does not predict species occurrence at a given locality, instead it is a broad description of the likelihood to disappear. Lowland attrition would affect short life-span species, range-shift gap would be important in groups with restricted distribution (for instance, those species living on the summit of the lower, drier island or rare species found in the cloud forest), while the effect of upland contraction would depend on the climatic conditions occurring on the summits of the different islands. On Tenerife, the low vulnerability to range-shift gaps of perennials can be attributed to a combination of low discontinuity and fairly high range, which is mainly related with the type of microhabitats where the species occur. Alternatively, the high vulnerability of perennials in Fuerteventura is probably the result of their short altitudinal range of occurrence, its location at the summit of the island and the absence of refugial sites (lava tunnels) in this old island. Annuals are more vulnerable to lowland attrition extinction in Gomera and Tenerife, due to their distribution at lower elevations. The higher vulnerability of colonists to upland attrition on Tenerife is explained by the fact that some species belonging to this group can tolerate the environmental conditions of its summit. Some of these species are restricted to summit areas (*Coscinodon cribosus* or the Canarian endemism *Grimmia curviseta*), while others (*Bryum dichotomum*) can tolerate a wide range of conditions. The vulnerability of colonists to upland extinction is also considerable on Gomera, where they are found at the highest elevation (see Table 1). They live on the summit of this island, mainly growing on salic volcanic domes where laurel forest cannot grow.

Overall, our study reveals the suitability of analyzing bryophytes on a regional scale according to biological attributes. There are two main justifications for our findings: (1) the probability of the occurrence of these microhabitats is dependent on regional gradients (Lohmus et al., 2007) and (2) bryophytes produce small and abundant propagules that can disperse at great distances. On local gradients, however, the variability of the occurrence of rare species may be strongly determined by the stochasticity of microsite occurrence and metapopulation behaviour (Rydin, 2009), and also the relative importance of dispersal *vs* microsite limitation determining the distribution of bryophyte populations on a local scale (Hedderson, 1992; Kimmerer, 2005).

An assessment of species vulnerability to climate change must integrate the information of species distribution with the different ability organisms have to disperse themselves (Guisan and Thuiller, 2005). In spite of its simplicity, the Colwell model takes onboard this challenge to some extent within a set of specific conditions: it provides a useful, prospective tool when the expected new conditions are largely driven by the elevation gradient, and when immigration from the surrounding areas to the lower part of the gradient is limited. Both conditions occur on oceanic islands with contrasting elevation gradients, such as the Canaries. This kind of analysis is, however, likely to underestimate the ability of species to remain on a given elevation belt through horizontal migration and, in the case of bryophytes, through finding microhabitat refugial sites. In the case of Canary Islands with a strong contrast between leeward and windward aspects this migration could be important. However, it may not be very relevant for species typical for the cloud forests which hardly would find moist conditions in leeward aspect. In fact, many of these laurel forest species are northern species, finding in the Canaries the southern limit of their distribution range. Also, any assessment of diversity in mountain areas should account for the effect of diminishing areas with elevation (Colwell and Lees, 2000). Our analysis is not expected to be strongly influenced by this area effect since we consider percentages of flora instead of richness, but the variability of these calculations is expected to increase stochastically with altitude. Other elements to be incorporated in the projection of the effect of climate change on bryofloras (biotic interactions, population dynamics, genetic drift) fall beyond our current stage of knowledge.

Considering a territorial context determined by insularity and the elevation gradient, our study shows that the expected temperature increase may be potentially deleterious for the different biological groups of bryophytes. We are aware, however, that our analysis does not consider changes in the precipitation regime, which remains rather uncertain in the climatic projections. Also, we did not find any climatic scenarios that considered the combined changes in temperature increase and the level of the cloud belt. We applied the Colwell model to bryophytes, but there is no reason why similar threats should not be found for other biological groups. In fact, our work illustrates the feasibility of preliminary assessments of the effect of climate change on groups of species where detailed information on their distribution and biology is not available. This assessment is reinforced by the incorporation of broad estimates of biological attributes. The scarcity of detailed studies on the impact of climate change on bryophytes (Bates et al., 2005; Molau and Alatalo, 1998) makes our analysis particularly relevant to a group where the rarity of some taxa make them particularly vulnerable to the new conditions. This study also supports initiatives for a comprehensive statement of the conservation status of these plants (Vanderpoorten and Hallingbäck, 2009) and detailed studies of the biology of the most threatened taxa. Nevertheless, the deviations from the general pattern of distribution observed by the different biological groups highlights the importance of considering microhabitats within regional conservation assessments.

Acknowledgements

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Appendix A. Species list indicating life strategy

Species	Life-strategy
Liverworts and hornworts	
Acanthocoleus aberrans (Lindenb. & Gottsche) Kruijt	Short-lived shuttle
Aneura pinguis (L.) Dumort.	Short-lived shuttle
Anthoceros agrestis Paton	Annual
Anthoceros caucasicus Steph.	Annual
Anthoceros punctatus L.	Annual
Aphanolejeunea azorica (V. Allorge & Jovet-Ast) Bernecker & Pocs	Short-lived shuttle
Aphanolejeunea microscopica (Taylor) A. Evans	Short-lived shuttle
Aphanolejeunea sintenisii Steph.	Short-lived shuttle
Asterella africana (Mont.) A. Evans	Short-lived shuttle
Athalamia spathysii (Lindenb.) S. Hatt.	Short-lived shuttle
Calypogeia arguta Nees & Mont.	Colonist
Calypogeia fissa (L.) Raddi	Colonist
Calypogeia sphagnicola (Arnell & J. Perss.) Warnst. & Loeske	Colonist
Calypogeia suecica (Arnell & J. Perss.) Müll. Frib.	Colonist
Cephalozia bicuspidata (L.) Dumort.	Colonist
Cephaloziella baumgartneri Schiffn.	Colonist
Cephaloziella calyculata (Durieu & Mont.) Müll. Frib.	Colonist
Cephaloziella dentata (Raddi) Steph.	Colonist
Cephaloziella divaricata (Sm.) Schiffn.	Colonist
Cephaloziella hampeana (Nees) Schiffn.	Colonist
Cephaloziella rubella (Nees) Warnst.	Colonist
Cephaloziella stellulifera (Taylor ex Spruce) Schiffn.	Colonist
Cephaloziella turneri (Hook.) Müll. Frib.	Colonist
Cololejeunea minutissima (Sm.) Schiffn.	Short-lived shuttle
Cololejeunea schaeferi Grolle	Short-lived shuttle
Colura calyptrifolia (Hook.) Dumort.	Short-lived shuttle
Conocephalum conicum (L.) Dumort.	Short-lived shuttle
Corsinia coriandrina (Spreng.) Lindb.	Short-lived shuttle
Diplophyllum albicans (L.) Dumort.	Colonist
Drepanolejeunea hamatifolia (Hook.) Schiffn.	Short-lived shuttle
Dumortiera hirsuta (Sw.) Nees	Long-lived shuttle
Exormotheca pustulosa Mitt.	Colonist
Fossombronia angulosa (Dicks.) Raddi	Annual
Fossombronia caespitiformis De Not. ex Rabenh.	Annual
Fossombronia echinata Macvicar	Annual
Fossombronia pusilla (L.) Nees	Annual
Frullania azorica Sim-Sim et al.	Long-lived shuttle
Frullania dilatata (L.) Dumort.	Long-lived shuttle
Frullania ericoides (Nees) Mont.	Long-lived shuttle
Frullania fragilifolia (Taylor) Gottsche et al.	Long-lived shuttle
Frullania microphylla (Gottsche) Pearson	Long-lived shuttle
Frullania polysticta Lindenb.	Long-lived shuttle
Frullania tamarisci (L.) Dumort.	Long-lived shuttle
Frullania teneriffae (F. Weber) Nees	Long-lived shuttle
Gongylanthus ericetorum (Raddi) Nees	Long-lived shuttle
Harpalejeunea molleri (Steph.) Grolle	Short-lived shuttle
Heteroscyphus denticulatus (Mitt.) Schiffn.	Perennial
Jubula hutchinsiae (Hook.) Dumort.	Perennial
Jungermannia atrovirens Dumort.	Colonist
Jungermannia callithrix Lindenb et Gottsche	Colonist
Jungermannia gracillima Sm.	Colonist
Jungermannia hyalina Lyell	Colonist
Jungermannia pumila With.	Colonist
Leiocolea turbinata (Raddi) H. Buch	Colonist
Lejeunea canariensis (Steph.) Steph.	Long-lived shuttle
Lejeunea cavifolia (Ehrh) Lindb.	Long-lived shuttle
Lejeunea eckloniana Lindenb.	Long-lived shuttle
Lejeunea flava (Sw.) Nees	Long-lived shuttle
Lejeunea lamacerina (Steph.) Schiffn.	Long-lived shuttle
Lejeunea mandonii (Steph.) Müll. Frib.	Long-lived shuttle
Lepidozia cupressina (Sw.) Lindenb.	Perennial
Lophozia bicrenata (Schmidel ex Hoffm.) Dumort.	Perennial
Lophocolea bidentata (L.) Dumort.	Perennial
Lophozia excisa (Dicks.) Dumort.	Colonist
Lophocolea fragrans (Moris & De Not.) Gottsche et al.	Perennial
Lophocolea heterophylla (Schrad.) Dumort.	Perennial
Lunularia cruciata (L.) Lindb.	Colonist
Mannia androgyna (L.) A. Evans	Short-lived shuttle
Marchantia paleacea Bertol.	Colonist
Marchantia polymorpha L.	Colonist
Marchesinia mackaii (Hook.) Gray	Perennial

Marsupella emarginata (Ehrh.) Dumort.	Colonist
Metzgeria conjugata Lindb.	Long-lived shuttle
Metzgeria furcata (L.) Dumort.	Colonist
Metzgeria leptoneura Spruce	Long-lived shuttle
Metzgeria temperata Kuwah.	Colonist
Microlejeunea ulicina (Taylor) A. Evans	Short-lived shuttle
Nardia geoscyphus (De Not.) Lindb.	Colonist
Nardia scalaris Gray	Short-lived shuttle
Oxymitra incrassata (Brot.) Sérgio & Sim-Sim	Annual
Phaeoceros carolinianus (Michx.) Prosk.	Annual
Phaeoceros laevis (L.) Prosk.	Annual
Phymatoceros bulbiculosus (Brot.) Stotler, W. T. Doyle & Crand.-Stotl.	Annual
Plagiochasma rupestre (J. R. Forst. & G. Forst.) Steph.	Short-lived shuttle
Plagiochila bifaria (Sw.) Lindenb.	Perennial
Plagiochila exigua (Taylor) Taylor	Perennial
Plagiochila maderensis Gottsche ex Steph.	Perennial
Plagiochila punctata (Taylor) Taylor	Perennial
Plagiochila stricta Lindenb.	Long-lived shuttle
Plagiochila virginica A. Evans	Perennial
Porella arboris-vitae (With.) Grolle	Long-lived shuttle
Porella canariensis (F. Weber) Underw.	Long-lived shuttle
Porella obtusata (Tayl.) Trevis.	Long-lived shuttle
Porella platyphylla (L.) Pfeiff.	Perennial
Radula aquilegia (Hook. f. & Tayl.) Gottsche et al.	Long-lived shuttle
Radula carringtonii J. B. Jack	Long-lived shuttle
Radula holtii Spruce	Colonist
Radula jonesii Bouman et al.	Long-lived shuttle
Radula lindenbergiana Gottsche ex C. Hartm.	Short-lived shuttle
Radula wichurae Steph.	Long-lived shuttle
Reboulia hemisphaerica (L.) Raddi	Short-lived shuttle
Riccia atromarginata Levier	Annual
Riccia bifurca Hoffm.	Annual
Riccardia chamedryfolia (With.) Grolle	Colonist
Riccia bifurca Hoffm.	Annual
Riccia cavernosa Hoffm.	Annual
Riccia ciliifera Link ex Lindenb.	Annual
Riccia ciliata Hoffm.	Annual
Riccia crinita Taylor	Annual
Riccia crozalsii Levier	Annual
Riccia crystallina L. emend. Raddi	Annual
Riccia glauca L.	Annual
Riccia gougetiana Durieu & Mont.	Annual
Riccia lamellosa Raddi	Annual
Riccia macrocarpa Levier	Annual
Riccardia multifida (L.) Gray	Colonist
Riccia nigrella DC.	Annual
Riccia papillosa Moris	Annual
Riccia sorocarpa Bisch.	Annual
Riccia subbifurca Warnst. ex Croz.	Annual
Riccia trabutiana Steph.	Annual
Riella affinis M. Howe & Underw.	Annual
Saccogyna viticulosa (L.) Dumort.	Perennial
Scapania compacta (A. Roth) Dumort.	Colonist
Scapania curta (Mart.) Dumort.	Colonist
Scapania gracilis Lindb.	Colonist
Scapania nemorea (L.) Grolle	Colonist
Scapania undulata (L.) Dumort.	Colonist
Southbya nigrella (De Not.) Henriq.	Short-lived shuttle
Southbya tophacea (Spruce) Spruce	Colonist
Sphaerocarpos michelii Bellardi	Annual
Sphaerocarpos texanus Austin	Annual
Targionia hypophylla L.	Short-lived shuttle
Telaranea azorica (H. Buch & Perss.) Pócs ex Schumacker & Váňa	Colonist
Telaranea europaea J. J. Engel & G. L. S. Merrill	Colonist
Tritomaria exsecta (Schmidel ex Schrad.) Loeske	Colonist
Mosses	
Acaulon mediterraneum Limpr	Colonist
Acaulon muticum (Hedw.) Müll. Hal.	Annual
Acaulon triquetrum (Spruce) Müll. Hal.	Annual
Aloina aloides (Koch ex Schultz) Kindb.	Colonist
Aloina ambigua (Bruch & Schimp.) Limpr.	Colonist
Aloina brevirostris (Hook. & Grev.) Kindb.	Colonist
Aloina humilis M. T. Gallego, M. J. Cano & Ros	Colonist
Aloina rigida (Hedw.) Limpr.	Colonist
Amphidium lapponicum (Hedw.) Schimp.	Colonist
Amphidium mougeotii (Schimp.) Schimp.	Colonist
Amphidium tortuosum (Hornsch.) Cufod.	Colonist
Anacolia webbii (Mont.) Schimp..	Long-lived shuttle
Andoa berthelotiana (Mont.) Ochyra	Perennial
Andreaea heinemannii Hampe & Müll. Hal.	Colonist
Anoectangium aestivum (Hedw.) Mitt.	Colonist
Anomobryum julaceum (Schrad. ex P.Gaertn., E. Meyer & Scherb.) Schimp.	Colonist
Antitrichia californica Sull.	Long-lived shuttle
Antitrichia curtipendula (Hedw.) Brid.	Long-lived shuttle
Archidium alternifolium (Hedw.) Mitt.	Short-lived shuttle
Atrichum angustatum (Brid.) Bruch & Schimp.	Short-lived shuttle
Atrichum undulatum (Hedw.) P. Beauv.	Short-lived shuttle
Aulacomnium androgynum (Hedw.) Schwägr.	Colonist
Barbula convoluta Hedw.	Colonist
Barbula unguiculata Hedw.	Colonist
Bartramia pomiformis Hedw. - P. T.	Short-lived shuttle
Bartramia stricta Brid.	Colonist
Brachymenium notarisii (Mitt.) A. J. Shaw	Colonist
Brachytheciastrum dieckii (Röll) Ignatov & Huttunen	Perennial
Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	Perennial
Brachythecium rutabulum (Hedw.) Schimp.	Perennial
Bryoerythrophyllum inaequalifolium (Taylor) R. H. Zander	Colonist
Bryum argenteum Hedw.	Colonist
Bryum canariense Brid.	Colonist
Bryum cellulare Hook.	Colonist
Bryum dichotomum Hedw.	Colonist
Bryum funckii Schwägr.	Colonist
Bryum gemmilucens R. Wilczeck & Demaret	Colonist
Bryum gemmiparum De Not.	Colonist
Bryum radiculosum Brid.	Colonist
Bryum ruderale Crundw. & Nyholm	Colonist
Bryum sauteri Bruch & Schimp.	Short-lived shuttle
Bryum subapiculatum Hampe	Colonist
Bryum tenuisetum Limpr.	Colonist
Bryum torquescens Bruch & Schimp.	Colonist
Bryum valparaisense Thér.	Colonist
Campylopus flexuosus (Hedw.) Brid.	Colonist
Campylopus fragilis (Brid.) Bruch & Schimp.	Colonist
Campylopus introflexus (Hedw.) Brid.	Colonist
Campylopus pilifer Brid.	Colonist
Campylostelium strictum Solms	Colonist
Ceratodon conicus (Hampe) Lindb.	Colonist
Ceratodon purpureus (Hedw.) Brid.	Colonist
Cheilothela chloropus (Brid.) Broth.	Colonist
Cirriphyllum crassinervium (Taylor) Loeske & M. Fleisch.	Perennial
Coscinodon cribrosus (Hedw.) Spruce	Colonist
Cratoneuron filicinum (Hedw.) Spruce	Perennial
Crossidium crassinerve (De Not.) Jur.	Colonist
Crossidium davidai Catches.	Colonist
Crossidium geheebii (Broth.) Broth.	Colonist
Crossidium squamiferum (Viv.) Jur.	Colonist
Cryphaea heteromalla (Hedw.) D. Mohr	Perennial
Cryptoleptodon longisetus (Mont.) Enroth	Perennial
Cyclodictyon laetevirens (Hook. & Taylor) Mitt.	Colonist
Cynodontium bruntonii (Sm.) Bruch & Schimp.	Colonist
Dialytrichia mucronata (Brid.) Broth.	Colonist
Dicranella heteromalla (Hedw.) Schimp.	Colonist
Dicranella howei Renauld & Cardot	Colonist
Dicranella varia (Hedw.) Schimp.	Colonist
Dicranoweisia cirrata (Hedw.) Lindb.	Colonist
Dicranum canariense Hampe ex Müll. Hal.	Colonist
Dicranum scoparium Hedw.	Perennial
Didymodon acutus (Brid.) K. Saito	Colonist
Didymodon australasiae (Hook. & Grev.) R. H. Zander	Colonist
Didymodon insulanus (De Not.) M. O. Hill	Colonist
Didymodon luridus Hornsch.	Colonist
Didymodon rigidulus Hedw.	Colonist
Didymodon sicculus M. J. Cano, Ros, García-Zamora & J. Guerra	Colonist
Didymodon tophaceus (Brid.) Lisa	Colonist
Didymodon umbrosus (Müll. Hal.) R. H. Zander	Colonist
Didymodon vinealis (Brid.) R. H. Zander	Colonist
Ditrichum pusillum (Hedw.) Hampe	Colonist
Ditrichum subulatum Hampe	Colonist
Encalypta streptocarpa Hedw.	Colonist
Encalypta vulgaris Hedw.	Colonist
Entosthodon attenuatus (Dicks.) Bryhn	Annual
Entosthodon commutatus Durieu & Mont.	Annual

Entosthodon convexus (Spruce) Brugués	Annual
Entosthodon durieui Mont.	Annual
Entosthodon fascicularis (Hedw.) Müll. Hal.	Annual
Entosthodon muhlenbergii (Turner) Fife	Annual
Entosthodon obtusus (Hedw.) Lindb.	Annual
Entosthodon pulchellus (H. Philib.) Brugués	Annual
Epipterygium tozeri (Grev.) Lindb.	Colonist
Eucladium verticillatum (With.) Bruch & Schimp.	Colonist
Fabronia pusilla Raddi	Perennial
Fissidens bryoides Hedw.	Colonist
Fissidens coacervatus Brugg.-Nann.	Colonist
Fissidens crassipes Wilson ex Bruch & Schimp.	Colonist
Fissidens crispus Mont.	Colonist
Fissidens curvatus Hornsch.	Colonist
Fissidens dubius P. Beauv.	Colonist
Fissidens exilis Hedw.	Colonist
Fissidens ovatifolius R. Ruthe	Colonist
Fissidens polyphyllus Wilson ex Bruch & Schimp.	Colonist
Fissidens rivularis (Spruce) Schimp.	Colonist
Fissidens serratus Müll. Hall.	Colonist
Fissidens serrulatus Brid.	Colonist
Fissidens sublimbatus Grout	Colonist
Fissidens taxifolius Hedw.	Colonist
Fissidens viridulus (Sw. ex anon.) Wahlenb.	Colonist
Funaria hygrometrica Hedw.	Fugitive
Funariella curviseta (Schwägr.) Sérgio	Colonist
Gigaspermum mouretii Corb.	Colonist
Goniomitrium seroi Casas	Colonist
Grimmia anodon Bruch & Schimp.	Colonist
Grimmia crinita Brid.	Colonist
Grimmia curviseta Bouman	Colonist
Grimmia decipiens (Schultz) Lindb.	Colonist
Grimmia funalis (Schwägr.) Bruch & Schimp.	Colonist
Grimmia laevigata (Brid.) Brid.	Colonist
Grimmia lisae De Not	Colonist
Grimmia longirostris Hook.	Colonist
Grimmia montana Bruch & Schimp.	Colonist
Grimmia ovalis (Hedw.) Lindb.	Colonist
Grimmia pulvinata (Hedw.) Sm.	Colonist
Grimmia ramondii (Lam. & DC.) Margad.	Colonist
Grimmia tergestina Tomm. ex Bruch & Schimp.	Colonist
Grimmia torquata Drumm.	Colonist
Grimmia trichophylla Grev.	Colonist
Grimmia ungeri Jur	Colonist
Gymnostomum aeruginosum Sm.	Colonist
Gymnostomum calcareum Nees & Hornsch.	Colonist
Gymnostomum viridulum Brid.	Colonist
Gyroweisia reflexa (Brid.) Schimp.	Colonist
Hedwigia ciliata (Hedw.) P. Beauv.	Long-lived shuttle
Hedwigia stellata Hedenäs	Long-lived shuttle
Heterocladium wulfsbergii I. Hagen	Perennial
Homalia lusitanica Schimp.	Perennial
Homalia webbiana (Mont.) Schimp.	Perennial
Homalothecium sericeum (Hedw.) Schimp.	Perennial
Hygroamblystegium varium (Hedw.) Lindb.	Perennial
Hypnum andoi A. J. E. Smith.	Perennial
Hypnum cupressiforme Hedw.	Perennial
Hypnum jutlandicum Holmen & E. Warncke	Perennial
Hypnum uncinulatum Jur.	Perennial
Imbribryum alpinum (Huds. ex With.) N. Pedersen	Colonist
Isothecium algarvicum W. E. Nicholson & Dixon	Perennial
Isothecium myosuroides Brid.	Perennial
Kindbergia praelonga (Hedw.) Ochyra	Perennial
Leptobryum pyriforme (Hedw.) Wilson	Colonist
Leptodon smithii (Hedw.) F. Weber & D. Mohr	Perennial
Leptodyctium riparium (Hedw.) Warnst.	Perennial
Leptophascum leptophyllum (Müll. Hal.) J. Guerra & M. J. Cano	Colonist
Leucobryum glaucum (Hedw.) Ångstr.	Perennial
Leucobryum juniperoideum (Brid.) Müll. Hal.	Perennial
Leucodon canariensis (Brid.) Schwägr.	Long-lived shuttle
Leucodon sciuroides (Hedw.) Schwägr.	Long-lived shuttle
Leucodon treleasei (Cardot) Paris	Long-lived shuttle
Microbryum davallianum (Sm.) R. H. Zander	Annual
Microbryum starckeanum (Hedw.) R. H. Zander	Colonist
Myurium hochstetteri (Schimp.) Kindb.	Perennial
Neckera cephalonica Jur & Unger	Perennial
Neckera complanata (Hedw.) Huebener	Perennial
Neckera intermedia Brid.	Perennial
Neckera pumila Hedw.	Perennial
Oedipodiella australis (Wager & Dixon) Dixon	Short-lived shuttle
Orthotrichum acuminatum H. Philib.	Colonist
Orthotrichum affine Schrad. ex Brid.	Colonist
Orthotrichum alpestre Bruch & Schimp.	Colonist
Orthotrichum cupulatum Hoffm. ex Brid.	Colonist
Orthotrichum diaphanum Schrad. ex Brid.	Colonist
Orthotrichum handiense F. Lara, Garilleti & Mazimpaka	Short-lived shuttle
Orthotrichum lyellii Hook. & Taylor	Short-lived shuttle
Orthotrichum pumilum Sw. ex anon.	Colonist
Orthotrichum rupestre Schleich. ex Schwägr.	Colonist
Orthotrichum tenellum Bruch ex Brid.	Colonist
Oxyrhynchium hians (Hedw.) Loeske	Perennial
Oxyrhynchium pumilum (Wilson) Loeske	Perennial
Oxyrhynchium speciosum (Brid.) Warnst.	Perennial
Pelekium atlanticum (Hedenäs) Hedenäs	Perennial
Philonotis caespitosa Jur.	Long-lived shuttle
Philonotis calcarea (Bruch & Schimp.) Schimp.	Long-lived shuttle
Philonotis fontana (Hedw.) Brid.	Perennial
Philonotis rigida Brid.	Long-lived shuttle
Philonotis tomentella Mol.	Long-lived shuttle
Physcomitrium pyriforme (Hedw.) Bruch & Schimp.	Annual
Plagiothecium nemorale (Mitt.) A. Gaeger	Perennial
Plagiomnium undulatum (Hedw.) T. J. Kop.	Perennial
Plasteurhynchium meridionale (Schimp.) M. Fleisch.	Perennial
Platyhypnidium riparioides (Hedw.) Dixon	Perennial
Pleuridium acuminatum Lindb.	Short-lived shuttle
Pleuridium subulatum (Hedw.) Rabenh.	Annual
Pogonatum aloides (Hedw.) P. Beauv.	Colonist
Pogonatum nanum (Hedw.) P. Beauv.	Colonist
Pohlia cruda (Hedw.) Lindb.	Colonist
Pohlia elongata Hedw.	Colonist
Pohlia melanodon (Brid.) A. J. Shaw	Colonist
Pohlia wahlenbergii (F. Weber & D. Mohr) A. L. Andrews	Colonist
Polytrichum commune Hedw.	Colonist
Polytrichastrum formosum (Hedw.) G. L. Sm.	Perennial
Polytrichum juniperinum Hedw.	Colonist
Polytrichum piliferum Hedw.	Colonist
Pseudocrossidium hornschuchianum (Schultz) R. H. Zander	Colonist
Pseudocrossidium revolutum (Brid.) R. H. Zander	Colonist
Pseudoscleropodium purum (Hedw.) M. Fleischer	Perennial
Pseudotaxiphyllum elegans (Brid.) Z. Iwats.	Colonist
Pterogonium gracile (Hedw. Sm.	Perennial
Ptychomitrium nigrescens (Kunze) Wijk & Margad.	Colonist
Ptychostomum capillare (Hedw.) D. T. Holyoak & N. Pedersen	Colonist
Ptychostomum donianum (Grev.) D. T. Holyoak & N. Pedersen	Colonist
Ptychostomum pallens (Sw.) J. R. Spence	Short-lived shuttle
Ptychostomum pallescens (Schleich. ex Schwägr.) J. R. Spence	Colonist
Ptychostomum imbricatulum (Müll. Hal.) D. T. Holyoak & N. Pedersen	Colonist
Ptychomitrium polyphyllum (Sw.) Bruch & Schimp.	Colonist
Ptychostomum pseudotriquetrum (Hedw.) J.R. Spence & H.P. Ramsay ex D.T. Holyoak & N. Pedersen	Colonist
Ptychostomum rubens (Mitt.) D. T. Holyoak & N. Pedersen	Colonist
Pylaisia polyantha (Hedw.) Schimp.	Short-lived shuttle
Racomitrium aciculare (Hedw.) Brid.	Colonist
Racomitrium aquaticum (Schrad.) Brid.	Colonist
Racomitrium ellipticum (Turner) Bruch & Schimp.	Colonist
Racomitrium heterostichum (Hedw.) Brid.	Colonist
Racomitrium lanuginosum (Hedw.) Brid.	Perennial
Rhabdoweisia fugax (Hedw.) Bruch & Schimp.	Colonist
Rhamphidium purpuratum Mitt.	Colonist
Rhynchostegiella bourgaeana (Mitt.) Broth.	Perennial
Rhynchostegiella litorea (De Not.) Limpr.	Perennial
Rhynchostegiella macilenta (Renauld & Cardot) Cardot	Perennial
Rhynchostegiella teneriffae (Mont.) Dirkse & Bouman	Perennial
Rhynchostegiella trichophylla Dirkse & Bouman	Perennial
Rhynchostegium confertum (Dicks.) Schimp.	Perennial
Rhynchostegium megapolitanum (Blandow ex F. Weber & D. Mohr) Schimp.	Perennial
Rhynchostegium murale (Hedw.) Schimp.	Perennial

Sanionia uncinata (Hedw.) Loeske	Perennial
Schistidium apocarpum (Hedw.) Bruch & Schimp.	Colonist
Schistidium confertum (*Funck*) *B. & S.*	Colonist
Schistidium flaccidum (De Not.) Ochyra	Colonist
Sciuro-hypnum plumosum (Hedw.) Ignatov & Huttunen	Perennial
Scleropodium cespitans (Wilson ex Müll. Hal.) L. F. Koch	Perennial
Scleropodium touretii (Brid.) L. F. Koch	Perennial
Scopelophila ligulata (Spruce) Spruce	Short-lived shuttle
Scorpiurium circinatum (Brid.) M. Fleisch. & Loeske	Perennial
Scorpiurium deflexifolium (Solms) M. Fleisch. & Loeske	Perennial
Sematophyllum substrumulosum (Hampe) E. Britton	Perennial
Syntrichia fragilis (Taylor) Ochyra	Colonist
Syntrichia laevipila Brid.	Colonist
Syntrichia montana Nees	Colonist
Syntrichia princeps (De Not.) Mitt.	Colonist
Syntrichia ruralis (Hedw.) F. Weber & D. Mohr	Colonist
Syntrichia virescens (De Not.) Ochyra	Colonist
Tetrastichium fontanum (Mitt.) Cardot	Perennial
Tetrastichium virens (Cardot) S. P. Churchill	Perennial
Thamnobryum alopecurum (Hedw.) Gangulee	Perennial
Timmiella barbuloides (Brid.) Mönk.	Colonist
Timmiella flexiseta (Bruch) Limpr.	Short-lived shuttle
Tortella alpicola Dixon	Colonist
Tortella flavovirens (Bruch) Broth.	Colonist
Tortella inflexa (Bruch) Broth.	Colonist
Tortella limbata (Schiffn.) Geh. & Herzog	Colonist
Tortella nitida (Lindb.) Broth.	Colonist
Tortella squarrosa (Brid.) Limpr	Colonist
Tortella tortuosa (Hedw.) Limpr.	Colonist
Tortula acaulon (With.) R. H.Zander	Colonist
Tortula ampliretis Crundw. & D. G. Long	Colonist
Tortula atrovirens (Sm.) Lindb.	Colonist
Tortula bogosica (Müll. Hal.) R. H. Zander	Colonist
Tortula bolanderi (Lesq. & James) R. H. Zander	Colonist
Tortula brevissima Schiffn.	Colonist
Tortula canescens Mont	Colonist
Tortula cuneifolia (Dicks.) Turner	Colonist
Tortula inermis (Brid) Mont.	Colonist
Tortula lindbergii Kindb. ex Broth	Colonist
Tortula marginata (Bruch & Schimp.) Spruce	Colonist
Tortula muralis Hedw.	Colonist
Tortula solmsii (Schimp.) Limpr.	Colonist
Tortula subulata Hedw.	Colonist
Tortula truncata (Hedw.) Mitt.	Colonist
Tortula vahliana (Schultz) Mont.	Colonist
Tortula viridifolia (Mitt.) Blockeel & A. J. E. Smith	Annual
Trichodon cylindricus (Hedw.) Schimp.	Colonist
Trichostomum brachydontium Bruch	Colonist
Trichostomum crispulum Bruch	Colonist
Ulota calvescens Wilson	Short-lived shuttle
Weissia condensa (*Voit*) *Lindb.*	Colonist
Weissia controversa Hedw.	Colonist
Weissia longifolia Mitt.	Colonist
Zygodon conoideus (Dicks.) Hook. & Taylor	Colonist
Zygodon rupestris Schimp. ex Lorentz	Colonist
Zygodon viridissimus (Dicks.) Brid.	Colonist

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