



# Extinction risk of threatened and non-threatened mosses: Reproductive and ecological patterns

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## ABSTRACT

For the conservation of species, it is crucial to predict extinction risk by discerning drivers such as biological traits and habitat specificity within the current context of environmental change. However, we lack comprehensive studies for threatened bryophytes that include comparisons to non-threatened ones. We aim to fill this gap and to detect biological traits related to extinction risk that provide new insights to develop conservation strategies for bryophytes. We analyzed the mosses of Spain ( $n = 771$ ) categorized into two groups (*threatened* and *non-threatened*) based on the IUCN Red List categories and considered seven variables related to reproduction and habitat preferences.

*Threatened* mosses show reproductive and habitat preference patterns that differ from those of the *non-threatened* species. The lack of reproduction, asexual reproduction, and monoicy are more common among *threatened* than *non-threatened* mosses. Habitat specialization, acidic and humid substrates are ecological characteristics associated with *threatened* mosses. In contrast, sexual reproduction and dioicy are more frequent among *non-threatened* species. Ecological features, such as the colonization of multiple habitats and wider altitudinal ranges, are also more often associated with *non-threatened* mosses.

Overall, we show that the extinction risk of mosses is associated with distinct reproductive traits and habitat preferences that may be related to the current context of global change and the natural rarity of some species.

## 1. Introduction

The vulnerability of biodiversity is increasing in the current scenario of rapid global change, which is leading to numerous local and global extinction events (Huang et al., 2012; Ceballos et al., 2015; Bergamini et al., 2019a; Humphreys et al., 2019). The extinction risk of species is not random but shows patterns that depend on the taxa studied (Schwartz and Simberloff, 2001; Ripple et al., 2017; Le Roux et al., 2019). It is also observed that threatened species exhibit different biological and ecological characteristics when compared

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with non-threatened species (Gustafsson, 1994; Richards et al., 2021). Specific biological traits (e.g., sexual system) and particular environments (e.g., wetlands) seem to be more susceptible to the impacts of human disturbances such as habitat destruction and climate change (Broennimann et al., 2006; Sodhi et al., 2008; Pacifici et al., 2015; Ripple et al., 2017). Consequently, species' biological traits and their habitat preferences are useful indicators to predict their vulnerability to threats or even their extinction risk (Ripple et al., 2017; Cooke et al., 2019; Richards et al., 2021).

The recognition of patterns in biological traits and habitat preferences that make species more prone to extinction is an important goal for establishing strategies for the management and conservation of biodiversity (Given and Norton, 1993; Ripple et al., 2017). In vascular plants, some studies reveal that reproductive failure, sexual system (monoicy or dioicy depending on the studied group), agamospermy, hydrophilia, life form (hemiscryptophytes), high pH soils, epiphytic habitat, narrow ecological niche and restricted geographic ranges are related to rarity and threatened status (Hodgson, 1986; Gustafsson, 1994; Murray et al., 2002; Domínguez et al., 2003; Broennimann et al., 2006; Sodhi et al., 2008; Humphreys et al., 2019; Le Roux et al., 2019). However, few studies have analysed the relationship between biological attributes, habitat preferences and extinction risks in bryophytes. To date, the most comprehensive studies or partial approaches have been focused on rare but not necessarily threatened species according to the IUCN Red List categories (Lampolahti and Syrjänen, 1992; Vitt and Belland, 1997; Laaka-Lindberg et al., 2000; Cleavitt, 2002, 2005; Söderström and During, 2005; Natcheva and Ganeva, 2009; Sérgio et al., 2013).

Bryophytes are the second largest group of embryophytes or land plants (Vanderpoorten and Goffinet, 2009) made up of three lineages, i.e., hornworts, liverworts and mosses (Donoghue et al., 2021). Compared to the other land plants, bryophytes present a haplo-diplophasic life cycle dominated by the haploid gametophyte (Vanderpoorten and Goffinet, 2009; Haig, 2016). Monoicous bryophytes possess bisexual gametophytes that ensure sexual reproduction and spore dispersal but also can favor haploid self-fertilization (Crawford et al., 2009; Haig, 2016). In contrast, dioicous bryophytes often fail to reproduce sexually while self-fertilization is uncommon (Haig, 2016; Alonso-García et al., 2020). Many bryophytes also reproduce asexually (Newton and Mishler, 1994; Frey and Kürschner, 2011), which facilitates their persistence under unfavorable environmental conditions (Söderström and During, 2005; Glime, 2017) or even dispersal at different spatial scales (Laenen et al., 2016; Tiselius et al., 2019). However, asexual reproduction as well as self-fertilization and sexual reproduction failure can affect the genetic variability of bryophytes (Roads and Longton, 2003; Eppley et al., 2007) and hamper their capacity to adapt to environmental changes (Magdy et al., 2016). Bryophytes can live in different and stressful environments (Ćosić et al., 2019) and often show wide distributions (Patiño and Vanderpoorten, 2018), but many species require specific environmental conditions at a local scale (e.g., very humid wet soils, shady forest understories) (Cleavitt, 2002). Their suitable microhabitats deteriorate drastically due to habitat destruction or fragmentation, climate change and over-exploitation of water resources (Koponen, 1992; Söderström, 2006; Hodgetts et al., 2019). Thus, bryophytes show different reproductive traits and possess environmental requirements that can influence their geographic range, population sizes or tolerance to human disturbances (Löbel et al., 2018) and therefore be related to their risk of extinction (Söderström and During, 2005).

Bryophytes are of great interest due to their role in the floristic composition, vegetation structure and ecosystem functioning of different ecosystems (Hallingbäck and Hodgetts, 2000). For instance, bryophytes are a relevant component in moist forests in temperate and subtropical montane regions and can be the predominant or codominant plants in wetlands and tundra (Hallingbäck and Hodgetts, 2000). Similarly, bryophytes play a crucial role as carbon sinks in temperate and Arctic zones, and they also contribute to water retention and soil fertility and stabilization in different habitats (Hallingbäck and Hodgetts, 2000; Deane-Coe and Stanton, 2017; Palozzi and Lindo, 2017). Likewise, the relatively simple anatomy of bryophytes makes them more vulnerable to atmospheric and soil contamination (Hallingbäck and Hodgetts, 2000) and therefore they become reliable bioindicators for the monitoring of water, soil and air quality (Hallingbäck and Hodgetts, 2000). However, many species of bryophytes are threatened at global and continental scales (Vanderpoorten and Hallingbäck, 2009; Hodgetts et al., 2019).

In recent decades, interest in evaluating the extinction risk and conservation status of bryophytes has led to the elaboration of Red Lists, which are one of the tools to further elaborate conservation priorities and management strategies (Rodrigues et al., 2006; Hodgetts et al., 2019). Red Lists are based on IUCN Red List criteria that primarily rely on population size, distribution, number of locations and trends (Brugués et al., 2014; Bergamini et al., 2019b; Hodgetts et al., 2019). However, the application of IUCN Red List criteria for bryophytes may be challenging due to difficulties in recognizing and obtaining empirical information on biological characters such as identification of individuals and estimation of generation length (Bergamini et al., 2019b). Similarly, current knowledge on basic data, such as distribution and population sizes, is poor for many bryophyte species (Hallingbäck, 2007; Garilieti and Albertos, 2012; Hodgetts et al., 2019). Hence, in parallel to the gathering of data required for the confident application of the IUCN Red List criteria, it is useful to analyze whether threatened and non-threatened bryophytes differ in their biological traits and habitat preferences. This approach can contribute to establish effective conservation strategies (Murray et al., 2002; Cleavitt, 2005; Natcheva and Ganeva, 2009; Hodgetts et al., 2019).

Our major aim is to analyse whether threatened bryophytes show common patterns regarding reproductive traits and habitat preferences in comparison to the pool of non-threatened species. We focus on mosses, the richest lineage of bryophytes (ca 12.000 species, Vanderpoorten and Goffinet, 2009), and specifically work with 771 species known from mainland Spain and the Balearic Islands (SW Europe). Our study group comprises a broad taxonomic spectrum (214 genera and 59 families) that represents 64% of the European moss flora (Casas et al., 2006). It integrates species related to distinct biogeographic elements (Arctic-alpine, Atlantic, Boreal, Mediterranean, Steppe, etc.) and different habitat preferences under distinct climatic regimes (Mediterranean, Alpine, Atlantic, Semi-desert). Its suitability as a target group is reinforced by the fact that the Spanish moss flora is subjected to the same multiple threats observed in the rest of Europe and worldwide (Hallingbäck and Hodgetts, 2000; Garilieti and Albertos, 2012; Hodgetts et al., 2019). Similarly, recent and detailed information is available on their reproductive biology, habitat preferences (Guerra and Cros, 2006, 2007, 2010; Guerra and Brugués, 2014, 2015, 2018) and conservation status (Brugués et al., 2014; Sáez et al., 2018a, 2018b).

We test the following working hypotheses: 1) Threatened species more often reproduce asexually or are non-reproductive compared with non-threatened species. Sexual reproduction is a costly process that requires additional resources (Haig, 2016; Glime, 2017) and different more specific environmental conditions compared to asexual reproduction (Glime, 2017). Thus, sexual reproduction could be easily hampered in habitats disturbed by humans (Wilson and Provan, 2003; Alvarenga et al., 2009) or under suboptimal environmental conditions, in the case of populations thriving close to the borders of their distribution range (Söderström and During, 2005; Glime and Bisang, 2017a). 2) A greater proportion of dioicous moss species are threatened compared to monoicous species. Separate sexes usually entail limitations in sporophyte and spore generation (Glime and Bisang, 2017b) which may impact species' dispersal (Cleavitt, 2005; Glime and Bisang, 2017b; Alonso-García et al., 2020). 3) Moss species occurring in a narrow range of environmental conditions (i.e., specialist species) are more prone to extinction than species occurring under a wide range of environmental conditions (Callaghan and Ashton, 2008; Richards et al., 2021). We specifically test whether threatened and non-threatened Spanish mosses differ in having or lacking sexual and asexual reproduction, the sexual system (dioicy and monoicy), the number of habitats colonized, habitat type (rocks, barks, etc.), substrate preferences (acidic, basic, saline, etc.), humidity (wet or dry substrates) and the extent of the altitude range.

## 2. Methods

### 2.1. Data collection

The study encompasses all moss species ( $n = 771$ ), threatened and non-threatened, growing in mainland Spain and the Balearic Islands (Table S1) but excluding the Canary Islands due to its highly distinct bryoflora (Mancebo et al., 2008). As principal references, we considered the Red List of the Bryophytes of peninsular Spain and the Balearic Islands (Brugués et al., 2014), the Red Book of the Threatened Bryoflora of Spain (Garillete and Albertos, 2012) and the Mosses of the Mediterranean, an annotated checklist (Ros et al., 2013). We also incorporated posterior amendments to the IUCN categories (Sáez et al., 2018a, 2018b) and new citations and species for the Iberian Peninsula and the Balearic Islands (Guerra and Cros, 2006, 2007, 2010; Guerra and Brugués, 2014, 2015, 2018; Ellis et al., 2018; Heribert et al., 2018). Data on reproduction and habitat preferences were taken from publications focused on Iberian and Balearic populations of the studied species (Guerra and Cros, 2006, 2007, 2010; Casas et al., 2006; Garillete and Albertos, 2012; Guerra and Brugués, 2014, 2015, 2018).

### 2.2. Data analysis

We classified moss species into two groups (Table S1): i) threatened (T,  $n = 180$  taxa), which includes taxa on the Spanish Red List (Brugués et al., 2014) assessed as Extinct (EX), Regional Extinct (RE), Critically Endangered (CR), Endangered (EN) or Vulnerable (VU); ii) not/near-threatened (No T,  $n = 591$ ), which includes taxa on the Spanish Red List assessed as Near Threatened (NT) or Least Concern (LC). We also include, within the not/near-threatened group, mosses not mentioned on the Red List (Brugués et al., 2014) that are common and abundant species previously evaluated as LC in the 2006 version of the Red List (Sérgio et al., 2006). They all

**Table 1**  
Descriptions of categorical variables.

Variable	Categories	Description
Type of reproduction	Sexual	presence of sporophyte in the Iberian populations
	Asexual	specialized organs and propagules (modified leaves, leaf apices, shoots, or branches, bulbils, gemmae, protonemal brood cells, and tubers)
	Both	sexual and asexual reproduction in the Iberian populations
	No reproduction	lack of sexual and asexual reproduction by specialized organs and propagules in the Iberian populations
Sexual system	Monoicous	bisexual gametophytes
	Dioicous	with archegonia and antheridia on separate plants
	Both	Including both monoicous and dioicous populations
Habitat specificity	Specialist	limited to one habitat type
	Generalist	growing in two or more habitat types
Habitat type (the most prevalent)	Aquatic	water bodies of rivers, springs, ponds, or other aquatic systems
	Terricolous	soils
	Saxicolous	rocks
	Terri-saxicolous	crevices and rocky soils
	Epiphyte	bark of trunks and branches, leaves
	Saprophyte	logs, litter
Habitat humidity	Wet	very humid habitats with permanent or temporary water including aquatic habitats
	Dry	habitats without permanent or temporary water or moisture
	Indifferent	without a marked preference
Substrate preferences	Acid	substrate (soil, rock, water) with $\text{pH} < 7$
	Alkaline(basic)	substrate (soil, rock, water) with $\text{pH} > 7$
	Saline	soils rich in Na, K, Cl, and $\text{CaSO}_4$ (gypsum soils)
	Indifferent	species without a marked trend

maintain a wide distribution and multiple populations as described in recent studies (Guerra and Cros, 2006, 2007, 2010; Guerra and Brugués, 2014, 2015, 2018) and are still considered non-threatened (see the 2001 redefinition of the IUCN categories, Pollock et al., 2003). Therefore, they were included in the second group (not/near-threatened, No T) as LC. Species classified as Data Deficient (DD) are not included in the present analyses.

To evaluate putative patterns in reproductive traits and habitat preferences in *threatened* and not/near-threatened mosses -hereafter referred as *non-threatened*-, we considered seven variables in total, six categorical variables (Table 1, Table S1) and one continuous, i.e., altitude range. The altitude range represents the interval of altitudes in which each species grows, and it is extracted from the minimum and maximum available altitude data from recent studies (Guerra and Cros, 2006, 2007, 2010; Guerra and Brugués, 2014, 2015, 2018). Taxa with no data for one of the variables were excluded from the respective analyses. We also excluded the phylogenetic relationships as an explanatory factor in our analyses since preliminary results from an ongoing study at the family level (see Calleja et al., 2021) reveal a negligible signal in agreement with previous studies focused on plants and extinction risk (Humphreys et al., 2019; Le Roux et al., 2019).

The numbers of species in the two groups, *threatened* (T) and *non-threatened* (No T), at each level of all categorical variables were compared using contingency tables and a Pearson's chi-squared test of independence. This type of analysis allows the inference of an association or interaction between the levels of the contrasted two variables (Queen et al., 2002). A post-hoc test was performed using Holm-Bonferroni correction for multiple comparisons (Abdi, 2010). To visualize the results of the analyses regarding the six categorical variables, the residuals of the chi-square test of independence were plotted. These residual values reflect whether the association between the levels of the contrasted variables is positive or negative and its magnitude (Queen et al., 2002).

The comparative analysis of the variable *altitude range* was performed with an ANOVA test after checking the normality and homogeneity of variances. The initial sample size ( $n = 591$ ) of the category No T was randomly reduced ( $n = 165$ ) to equal that of the category T with available altitude range data ( $n = 165$ ).

For contingency tables and data description of the analysis see Supplementary Material Tables S1, S2, S3, S4, S5, S6, S7, and S8. Analyses were performed using car (Fox and Weisberg, 2019), chisq.posthoc.test (Ebbert, 2019), corrplot (Wei and Simko, 2021), DescTools (Andri, 2021), ggpubr (Kassambara, 2020), psych (Revelle, 2021), RVAideMemoire (Hervé, 2021), and stats libraries in R Statistical Software (R Core Team, 2019).

### 3. Results

Our results show that *threatened* and *non-threatened* mosses differ in their reproductive traits and habitat preferences, except for type of habitat (Table 2; Supplementary Material Tables S2, S3, S4, S5, S6, S7, and S8).

As we expected, *threatened* mosses lack explicit means of reproduction or primarily rely on asexual reproduction in greater proportions than those of *non-threatened* mosses. However, and contrary to our working hypothesis, the proportion of monoicous species is greater among *threatened* mosses than expected (Fig. 1a and b). In contrast, *non-threatened* mosses rely relatively more often on sexual reproduction and less on the asexual mode than *threatened* mosses. In addition, dioicy in *non-threatened* mosses is more common than monoicy compared to *threatened* mosses (Fig. 1a and b).

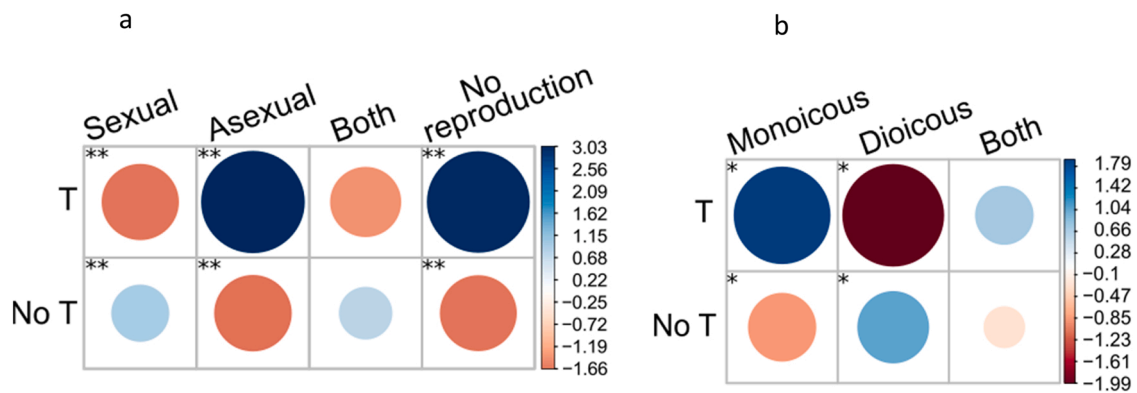
In agreement with our working hypothesis, there is a strong association between *threatened* and *non-threatened* mosses and habitat specificity, habitat humidity and substrate type (Table 2, Figs. 2 and 3). *Threatened* mosses comprise a greater proportion of specialist species than *non-threatened* mosses (Fig. 2a). *Threatened* mosses also comprise a greater proportion of species associated with habitats with high humidity (Fig. 3a) despite the lack of support for the positive association with aquatic habitats (Fig. 2b). *Threatened* mosses show a negligible relationship with stressful substrata such as saline soils (Fig. 3b) but they show a greater proportion of species associated with acidic soils than *non-threatened* mosses (Fig. 3b). Conversely, *non-threatened* mosses include a greater proportion of generalist species, show a positive association with dry habitats and a negative association with wet habitats and acid substrates (Figs. 2 and 3).

Finally, *threatened* and *non-threatened* mosses significantly differ ( $p < 0.001$ ) in their altitude ranges (Fig. 4 and Table 2 and Table S8). Despite the overlapping of the total altitude ranges, the mean and median altitude ranges are narrower in *threatened* than in *non-threatened* species (Fig. 4 and Table S8).

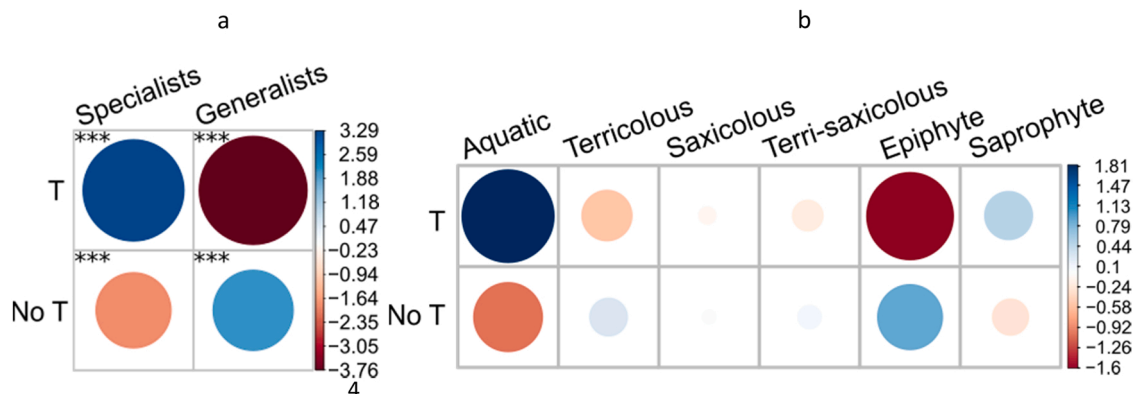
**Table 2**

Analysis of reproduction and habitat preferences of mosses of peninsular Spain and the Balearic Islands. F = test F(ANOVA), n = sample size (n),  $X^2$  = Chi-square.

	n	Statistic	p-value
Type of reproduction	771	$X^2 = 29.858$	< 0.001
Sexual system	619	$X^2 = 9.514$	0.009
Habitat specificity	771	$X^2 = 32.33$	< 0.001
Habitat type	753	$X^2 = 8.348$	0.138
Habitat humidity	770	$X^2 = 14.407$	< 0.001
Substrate preferences	766	$X^2 = 16.875$	< 0.001
Altitude range	330	F = 169.1	< 0.001



**Fig. 1.** Reproductive characteristics of mosses of mainland Spain and the Balearic Islands. Plots show the residuals of Pearson chi-squared analysis for type of reproduction (1a) and sexual system (1b) for the two moss groups: T (threatened) includes EX (Extinct), RE (Regional Extinct), CR (Critically Endangered), EN (Endangered), and VU (Vulnerable); and No T (not/near-threatened) includes NT (Near Threatened) and LC (Least Concern). The y-axis on the right reflects the range of variation of all the residuals in the contingency table. Within each cell, the size of the circle is related to the absolute value of the residual; the bigger the circle, the stronger the association. In blue: positive residuals, showing a positive association between the corresponding row and column, and in red: negative residuals, showing a negative association between the corresponding row and column. Levels of significance of the post-hoc test are shown: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , and \*\*\* =  $p < 0.001$ . They refer to the comparisons among the cells of the same column. Post-hoc residuals and p-values are shown in [Tables S2b and S3b](#).



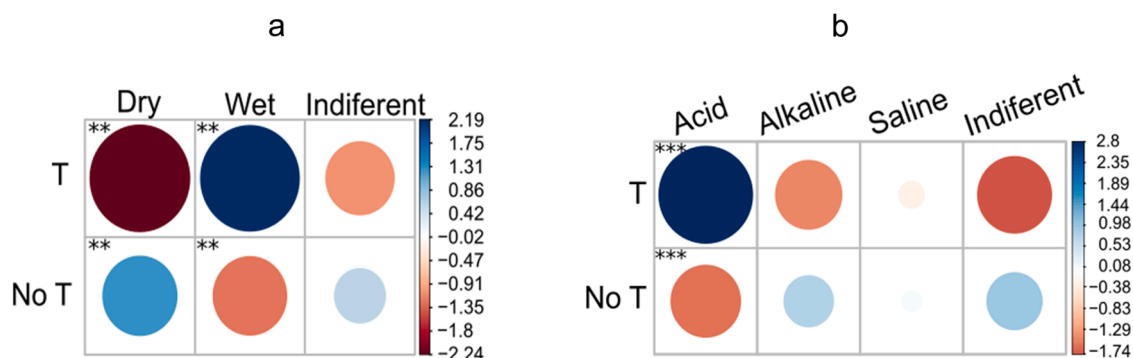
**Fig. 2.** Habitat specialization and type of habitat of mosses of mainland Spain and the Balearic Islands. Plots show the residuals of Pearson chi-squared analysis for habitat specialization (a) and type of habitat (b) for the two moss groups: T (threatened) includes EX (Extinct), RE (Regional Extinct), CR (Critically Endangered), EN (Endangered), and VU (Vulnerable); and No T (not/near-threatened) includes NT (Near Threatened) and LC (Least Concern). The y-axis on the right reflects the range of variation of all the residuals in the contingency table. Within each cell, the size of the circle is related to the absolute value of the residual; the bigger the circle, the stronger the association. In blue: positive residuals, showing a positive association between the corresponding row and column, and in red: negative residuals, showing a negative association between the corresponding row and column. Levels of significance of the post-hoc test are shown: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , and \*\*\* =  $p < 0.001$ . They refer to the comparisons among the cells of the same column. For post-hoc residuals and p-values see [Tables S4b, S5b](#).

## 4. Discussion

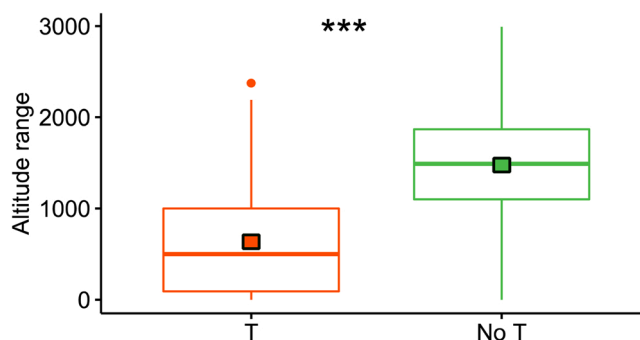
### 4.1. Reproductive traits

*Threatened* mosses from peninsular and Balearic Spain, in comparison with *non-threatened* ones, comprise a greater proportion of species that lack reproduction, either sexual or asexual, or rely significantly on specific asexual reproductive mechanisms. Our results agree with previous findings in different groups of animals and vascular plants (Kunin and Gaston, 1993; Silvertown, 2008; King et al., 2012). This is also true for bryophytes, but with a focus on rare species without explicitly considering their conservation status (Laaka-Lindberg et al., 2000; Söderström and During, 2005). Those species without any type of reproduction might eventually propagate since the gametophyte of all mosses has the ability to generate new individuals by fragmentation (Crawford et al., 2009; Frey and Kürschner, 2011).

The lack of explicit means of reproduction or just having the asexual one of threatened mosses can be the consequences of threats. Human disturbances, especially intense or recurrent ones, may limit the development of sporophytes and specific mechanisms for



**Fig. 3.** Habitat humidity and substrate preferences of mosses of mainland Spain and the Balearic Islands. Plots show the residuals of Pearson chi-squared analysis for habitat humidity (a) and substrate preferences (b) for the two moss groups: T (threatened) includes EX (Extinct), RE (Regional Extinct), CR (Critically Endangered), EN (Endangered) and VU (Vulnerable); and No T (not/near-threatened) includes NT (Near Threatened) and LC (Least Concern). The y-axis on the right reflects the range of variation of all the residuals in the contingency table. Within each cell, the size of the circle is related to the absolute value of the residual; the bigger the circle, the stronger the association. In blue: positive residuals, showing a positive association between the corresponding row and column, and in red: negative residuals, showing a negative association between the corresponding row and column. Levels of significance of the post-hoc test are shown: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , and \*\*\* =  $p < 0.001$ . They refer to the comparisons among the cells of the same column. For post-hoc residuals and p-values see Table S6b and S7b.



**Fig. 4.** Altitude range of mosses of mainland Spain and the Balearic Islands. T (threatened) includes EX (Extinct), RE (Regional Extinct), CR (Critically Endangered), EN (Endangered) and VU (Vulnerable); and No T (not/near-threatened) includes NT (Near Threatened) and LC (Least Concern). In the boxplot diagrams, mean and median altitude ranges are represented by quadrats and horizontal lines, respectively; the boxes show the interquartile range (distance from 25th to 75th percentile); the whiskers indicate the minimum (0th percentile) and maximum (100th percentile) excluding outliers (shown as points). \*\*\* =  $p < 0.001$ . ANOVA values are shown in Table 2 and Table S8.

asexual reproduction as well as population establishment (Zechmeister and Moser, 2001). For instance, pollution, habitat and population fragmentation can impair sexual reproduction in bryophytes either by direct impact on individuals (e.g. pollution, see Nash and Nash, 1974) or by the concomitant population decline and genetic erosion (Wilson and Provan, 2003; Korpelainen et al., 2012). This could be the case for the wetland species such as *Meesia triquetra* (L. ex Jolycl.) Ångstr., that grows in highly fragmented habitats (Infante and Heras, 2012). Stressful environments can also promote asexual reproduction in threatened species (Nash and Nash, 1974; Newton and Mishler, 1994). However, as occurs in vascular plants and other organisms (de Meeûs et al., 2007; Niklas and Cobb, 2017), asexual reproduction entails the absence of recombination that may result in lower genetic variability in bryophytes (Shaw, 1999; Niklas and Cobb, 2017) despite the occurrence of somatic mutations (Newton and Mishler, 1994; Klekowski, 1997). In turn, low genetic variability increases the species' vulnerability (Lei, 2010; Hodgetts et al., 2019). Moreover, the significantly larger size of asexual diaspores limits dispersal distances and colonization capacities (Tiselius et al., 2019) and makes bryophytes more vulnerable to habitat fragmentation (Löbel and Rydin, 2009).

Alternatively to the effects of environmental changes induced by human disturbances, the absence of reproduction or the predominance of asexual reproduction can be inherent traits that may render a species vulnerable (Gaston, 1994; Söderström and During, 2005). Numerous species assessed as threatened show very narrow distributions or scarce populations but are driven by natural causes (Pärtel et al., 2005; Raphael and Molina, 2013). Natural rare animals or plants including bryophytes (Gaston, 1994; Söderström and During, 2005) often show poor sexual performance or rely only on asexual reproduction, like those living at the edge of their distribution ranges and thus growing far from their ecological optimum (Kunin and Gaston, 1993; Söderström and During, 2005; Silvertown, 2008; Natcheva and Ganeva, 2009). Under such conditions, investment into asexual reproduction is often lower than in sexual reproduction in bryophytes (Haig, 2016; Glime, 2017). Thus, bryophytes show a remarkable diversity of asexual propagules

that enable them to survive in suboptimal conditions (Frey and Kürschner, 2011; Maciel-Silva and Pôrto, 2014). This could be the case for the scarce Iberian populations of cold temperate or alpine mosses such as of *Didymodon asperifolius* (Mitt.) H.A.Crum, Steere and L. E. Anderson (Jiménez, 2012), *Pohlia filum* (Schimp.) Martensson (Guerra, 2012) and *Tortella alpicola* Dixon (Rams et al., 2012). In these examples of mosses with only asexual reproduction in Spain, human threats are absent, and their conservation status is related only to their natural rarity (Söderström and During, 2005; Garilleti and Albertos, 2012). The origin of their current small populations might be related either to past environmental changes and geographical range oscillations (Frahm, 2012; Kyrkjeeide et al., 2014) or to limited and recent long-distance dispersal events (Sotiaux et al., 2006; Vigalondo et al., 2019; Flagmeier et al., 2020).

In contrast, *non-threatened* mosses show a greater proportion of species with sexual reproduction and a lower proportion with asexual reproduction than *threatened* species. These characteristics are shared with other non-threatened organisms including vascular plants (Kunin and Gaston, 1993) and bryophytes (Laaka-Lindberg et al., 2000; Söderström and During, 2005). These results were expected due to the positive association of sexual reproduction with genetic variability (Crow, 1994), dispersal capacity (Crawford et al., 2009) and population sizes (Lande, 1988).

Regarding the sexual system, monoicy is more common than expected in Spanish *threatened* mosses. We envisaged the opposite result i.e., a positive association between *threatened* mosses and dioicy. The expected limited sexual reproduction between individuals of separated sexes (Nath and Asthana, 2001; Maciel-Silva and Pôrto, 2014; Glime and Bisang, 2017b) may have led species and populations to be more susceptible to extinction risk (Lauterbach et al., 2012; Shivanna, 2015; Walas et al., 2018). In fact, dioicy in vascular plants, bryophytes, and other organisms is usually associated with asexual reproduction (Longton and Schuster, 1983; During, 2007; Haig, 2016), which in turn compensates for sexual reproduction limitations (Glime and Bisang, 2017a; 2017b). However, comparative phylogenetic analyses on liverworts (Laenen et al., 2016) and mosses (Crawford et al., 2009) reveal no significant correlation between dioicy and asexual reproduction. Mosses also show remarkable lability in the expression of the sexual system and asexual reproduction that remains unexplained (Crawford et al., 2009). Thus, further studies on the influence of intrinsic but also extrinsic factors such as the environmental context and human disturbances on the reproductive traits might explain the positive relationship detected between dioicy and asexual reproduction in certain bryophytes and local bryofloras (Longton and Schuster, 1983; Glime and Bisang, 2017b).

In our study, the higher proportion of monoicy observed in *threatened* mosses than in *non-threatened* might be counterintuitive since sporophyte and spore production in monoicous bryophytes is greater than in dioicous ones (Longton, 2006; Natcheva and Ganeva, 2009; Glime and Bisang, 2017b). However, a high frequency of monoicy has been previously reported in rare and threatened bryophytes (Longton, 1992; Laaka-Lindberg et al., 2000; Söderström and During, 2005; Natcheva and Ganeva, 2009; but see Sérgio et al., 2013). It is worth noting that, if self-fertilization takes place in a monoicous bryophyte, the offspring will be genetically identical to the haploid mother plant, despite sexual reproduction (Haig, 2016). This is because monoicy in bryophytes implies the union of gametes originating from mitosis from gametangia within the same gametophyte. Since gametes possess identical genetic information, there must be homozygosity at every locus of the embryo (Crawford et al., 2009). This fact is unparalleled in land plants characterized by a sporophyte-dominant life cycle (Haig, 2016). Some works (Roads and Longton, 2003; Eppley et al., 2007) have revealed that monoicy reduces the genetic variability in bryophytes, which in turn might hamper their phenotypic plasticity and capacity to adapt to environmental changes (Magdy et al., 2016). Thus, the detrimental effects of reproductive traits such as monoicy and asexual reproduction on genetic variability could be an underlying mechanism driving the vulnerability of mosses (Longton, 1992, 2006; Honnay and Bossuyt, 2005).

The observed higher proportion of dioicous mosses in *non-threatened* than in *threatened* species has previously been noted in other areas, both on mosses (Longton, 1992) and liverworts (Söderström and During, 2005). In fact, the number of dioicous bryophytes is greater than that of monoicous (Hedenäs and Bisang, 2011; Glime and Bisang, 2017b) whereas vascular plants show the opposite pattern (Renner and Ricklefs, 1995). In bryophytes, however, the generation of sporophytes and spores is noticeably more common in monoicous than in dioicous species (Glime and Bisang, 2017b) whereas sporophytes have never been found in many dioicous species (Cronberg, 1991; Glime, 2017). It could therefore be paradoxical that non-threatened mosses possess a sexual system that involves difficulties for sporophyte development. However, the advantages of sexual reproduction are not impeded. Bryophytes, like vascular plants, can thrive with eventual sexual reproduction events that ensure genetic variability and dispersal, which are relevant factors in the dynamic processes of bryophyte populations (Bengtsson, 2003; Söderström and During, 2005; Johnson and Shaw, 2015; Haig, 2016).

#### 4.2. Habitat preferences

*Threatened* mosses, in agreement with previous works on rare bryophytes (Cleavitt, 2005; Söderström, 2006), include a greater proportion of specialists than *non-threatened*. As observed in other organisms (Tilman et al., 2017; Cooke et al., 2019; Richards et al., 2021), bryophytes with a high habitat specificity, i.e., specialist species, are more vulnerable to habitat destruction since they fail to thrive elsewhere (Söderström, 2006; Bergamini et al., 2009). In contrast, *non-threatened* mosses include a greater proportion of generalist species defined as growing in more than one habitat. This ability allows them to be more abundant in terms of population size and geographical range (Slatyer et al., 2013), although reproduction and dispersal success may significantly differ (Herben, 1994). Thus, our comparison indicates that habitat specificity in mosses arises as a clear factor associated with the risk of extinction as observed in vascular plants (Broennimann et al., 2006) and different groups of animals (Cooke et al., 2019; Richards et al., 2021).

Unexpectedly, no habitat type stands out as hosting a significant proportion of *threatened* or *non-threatened* species. Our results differ from those of previous works in which epiphytic and aquatic environments host higher numbers of threatened species than other habitats (Vitt and Belland, 1997; Berg et al., 2002; Natcheva and Ganeva, 2009; Hodgetts et al., 2019). However, our analyses also

reveal that, compared with *non-threatened* moss species, a greater proportion of *threatened* mosses live in humid habitats rather than in dry ones. This result agrees with previous works focused on bryophytes (Sérgio et al., 2013) and vascular plants (Domínguez et al., 2003) that encompass a wide geographical range with multiple habitat and climate types. In the same line, our results may be related to current alterations of wetlands (including riverbanks and riverbeds, springs, permanent and seasonal ponds) in terms of their physical structure, hydrologic cycle, and water quality in Spain (Casado et al., 1992; Ibáñez and Caiola, 2013) and other regions (Hodgetts et al., 2019; Xu et al., 2019). In Spain, local studies have shown the demise of populations and an increase in *threatened* bryophytes linked to wet habitats (Vieira et al., 2005; Sáez et al., 2018a, 2018b). Likewise, the high discontinuity and reduced extent of wet microhabitats in Mediterranean Spanish landscapes (Casado et al., 1992) may limit dispersal success and constrain the number of colonized areas, a key criterium to establish IUCN Red List categories (Hodgetts et al., 2019).

In contrast, *non-threatened* mosses are more often associated with dry environments. These species show more drought-resistant spores that in turn exhibit a greater chance to survive a long period of drought after dispersal, thus increasing establishment success compared to mosses restricted to wet conditions (Wiklund and Rydin, 2004). We note that this clear difference between *threatened* and *non-threatened* species could change in extra-Mediterranean territories where the prevalence of humid environments can be markedly greater and thus, rare and endangered species may be constrained to dry habitats (Silva and Germano, 2013).

Chemical properties of soils are also crucial for many bryophytes (Dirkse and Martakis, 1992; Eldridge and Tozer, 2009). However, contrary to previous works (Casas et al., 1992), the *threatened* mosses lack a significant association with saline substrates whereas the opposite is true for vascular plants (Domínguez et al., 2003). Even though these peculiar environments host unique sets of bryophytes (Guerra et al., 1995), they include both *threatened* and *non-threatened* species (Guerra and Cros, 2006, 2007, 2010; Guerra and Brugués, 2014, 2015, 2018). Our results also show a strong association of *threatened* mosses with acidic substrates. Other spore-plants like ferns seem to be favored in acidic lithologies that retain more water compared to alkaline environments, thus favoring processes that require water such as reproduction (Pausas and Sáez, 2000). In fact, ferns from the Iberian Peninsula show a higher diversity in acidic substrata including rare and threatened species thriving far from their ecological and geographical optimum (Moreno and Lobo, 2008). Along the same lines, many acidophilous and threatened mosses in Spain reflect a finicolous character i.e., they show isolated populations at the edge of wide continental (or even trans-continental) distributions e.g., *Dichelyma falcatum* (Hedw.) Myrin, *Polytrichastrum longisetum* (Sw. ex Brid.) G.L.Sm., and *Schistidium occidentale* (E.Lawton) S.P.Churchill (Garilleti and Albertos, 2012). Another plausible explanation could be the ecophysiological constraints on spore establishment on low pH substrates for those bryophytes growing in mesic and dry environments (Wiklund and Rydin, 2004). At low pH, spores demand more days of moisture to germinate, which in turn reduces establishment success (Wiklund and Rydin, 2004). Thus, the vulnerability of acidophilous mosses could gain relevance within the current scenario of global warming and alterations to habitats including the wet zones (Estrela et al., 2012).

Regarding the altitude range, as expected, *threatened* mosses show narrower altitudinal ranges than *non-threatened* mosses. This fact agrees with the restricted distributional range of Iberian populations of many threatened mosses that occur in few localities, e.g., *Sphagnum fuscum* (Schimp.) H.Klinggr. (Brugués and Ruiz, 2012) and *Brachythecium laetum* (Brid.) Schimp. (Orgaz, 2012). The altitude range, like habitat specificity, is related to the extinction risk of flowering plants (Domínguez et al., 2003) and other organisms (Purvis et al., 2000). The altitude range can reflect the area and the ecological niche breadth that species are able to occupy (Körner, 2007). The ecological niche breadth is a crucial factor in species vulnerability (Cleavitt, 2005; Broennimann et al., 2006; Richards et al., 2021), especially considering that one of the main threats to bryophytes as well as to the rest of biodiversity is habitat modification and destruction (Tilman et al., 2017; Hodgetts et al., 2019). Narrow altitudinal ranges of mosses may reveal an inability to adapt to different habitats, climate regimes, and environmental disturbances including human-induced ones (Cleavitt, 2005; Pykälä, 2019). Similarly, the restricted distributional range of *threatened* mosses could be linked to reproduction failures and dispersal limitations related to their natural rarity (Söderström and Daring, 2005; Natcheva and Ganeva, 2009).

## 5. Conclusions

In sum, we found that *threatened* and *non-threatened* moss species differ in their reproductive traits and habitat preferences. The patterns observed may be a consequence of human disturbances or due to inherent traits of the species, but further studies are needed to discern which factors are most relevant.

*Threatened* mosses, compared to *non-threatened*, are relatively more often monoicous, and more often lack reproduction or reproduce only asexually. In contrast, *non-threatened* mosses more often lack asexual reproduction and are more often dioicous.

*Threatened* mosses comprise a greater proportion of specialist species than *non-threatened*, and are more often associated with acidic and humid substrates, and narrow altitudinal ranges. Conversely, *non-threatened* mosses comprise a greater proportion of generalist species and more often thrive in wide altitudinal ranges.

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## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02254](https://doi.org/10.1016/j.gecco.2022.e02254).

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