






RESEARCH ARTICLE

Factors determining bryophyte species richness and community composition on insular siliceous erratic boulders in calcareous landscapes

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Abstract

Aim: Pleistocene erratic boulders are rocks that were relocated by glaciers during the Ice Ages. When their geology differs from the geology of the landscape that surrounds them, erratic boulders form habitat islands for regionally rare, edaphically specialised, rock-dwelling cryptogams (bryophytes, ferns and lichens). Such boulders constitute terrestrial model systems for exploring island biogeographic predictions and the effect of environmental variables on species diversity and community composition, which we studied in order to provide basic knowledge of the ecology, with relevance for the conservation, of these unusual island systems.

Location: Siliceous erratic boulders in the calcareous Swiss Plateau and Jura Mountains.

Methods: For 160 erratic boulders we recorded all bryophyte species and a diverse set of environmental variables. For all species and for specialist species (acidophile rock-dwellers) separately, we analysed species–area relationships and nestedness, and explored relationships between environmental variables, species diversity and community composition.

Results: We found 138 bryophyte species, 19 of which were specialists of erratic boulders. A steeper species–area curve for boulder specialists than for total species richness underlined the island properties of boulders for specialist species. Large boulders were more likely to harbour numerous boulder specialists and communities on small boulders were nested within the communities present on large boulders. However, at the landscape level small boulders contributed more specialist species than a few large boulders of the same surface area. Erratic boulders near settlements were less likely to harbour boulder specialists. Boulders in open land harboured different and more specialist species than boulders in forests.

Conclusions: Large undisturbed erratic boulders in open land harbour rare bryophyte communities with a large number of specialist species. Conservation should thus prioritise this type of boulders. Furthermore, conserving large boulders is logistically

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easier, and they may function as flagships for small boulders that also contribute to the biodiversity within landscapes.

KEYWORDS

Biodiversity, conservation biology, erratic blocks, geodiversity, island biogeography, mosses, nestedness, SLOSS, species–area relationship

1 | INTRODUCTION

Geodiversity, the abiotic diversity of the earth's surface, has a pivotal, yet rarely explicitly studied, influence on biodiversity (Tukiainen et al., 2019; Alahuhta et al., 2020). In particular, small geosites that have insular properties, such as isolated cliffs or springs, can contribute specialist species to the species pool of a larger landscape that otherwise lacks the geosites' special abiotic properties essential for the survival of specialist species (Hjort et al., 2015; Itescu, 2019). Pleistocene erratic boulders — rocks that were relocated by glaciers during the Ice Ages — are such small geosites. Erratic boulders contribute greatly to the reconstruction of the earth's history and climate (Imbrie & Imbrie, 1986), but they also contribute to biodiversity. In particular, this is the case in landscapes with bedrock that contrasts the rock type of erratic boulders, where the boulders often harbour regionally rare rock-dwelling cryptogams (bryophytes, ferns and lichens), for example, on the European sand plain between Belgium and Estonia, where erratic boulders are the only naturally occurring hard rock habitats (Krawiec, 1938; Wächter, 1996; Colpa & van Zanten, 2006). Further cases of erratic boulders that constitute insular habitats can be found on the siliceous bedrock of central Finland, where calcicole rock-dwelling bryophytes are confined to calcareous erratic boulders (Virtanen & Oksanen, 2007), and on the calcareous bedrock of the French and Swiss Jura Mountains, where calcifuge rock-dwelling bryophytes are confined to siliceous erratic boulders (Meylan, 1912; Philippe, 2010).

Among the large variety of insular systems that have been studied for exploring aspects of island biogeography (MacArthur & Wilson, 1967; Itescu, 2019), erratic boulders unite some properties that are favourable for their exploration as a terrestrial island model system. Their small size and restricted habitat diversity allows collecting complete species lists and a more accurate description of environmental conditions than on large islands. Furthermore, as boulders do not result from habitat fragmentation, their species composition is likely to be near an equilibrium state. The fact that boulders harbour specialist and non-specialist species allows comparison of island and mainland species–area relationships derived from the same patches of habitat. Nonetheless, studies on insular erratic boulders are scarce. In Swedish forests, bryophyte species richness on 216 siliceous erratic boulders was found to be positively related to boulder area, within-boulder habitat diversity and base-rich litter of the tree species surrounding the boulders (Weibull, 2001; Weibull & Rydin, 2005). Virtanen and Oksanen (2007) similarly found a positive link between boulder size and species richness and additionally reported a weak positive effect of connectivity to other boulders in a data

set comprising 288 erratic calcareous boulders in Finnish forests. Kimmerer and Driscoll (2000), however, found neither boulder size nor connectivity among boulders to be related to boulder species richness on 39 granitic erratic boulders in the US state of New York. While these studies exclusively considered boulders in forests, the factors shaping bryophyte diversity of boulders at the landscape level appear not to be studied so far.

In the present study, our main aim is to determine the factors that influence bryophyte diversity and community composition on siliceous erratic boulders in the calcareous Swiss lowlands in forested and non-forested areas. Furthermore, we discuss the implications of our findings for conservation, because the special vegetation of erratic boulders is threatened in many places, due to depletion of boulders (Gonggrijp, 2000; Akçar et al., 2011), declines and regional rarity of their specialist species (Wächter, 1996; Ulvinen et al., 2002; Colpa & van Zanten, 2006; Siebel et al., 2013; Ingerpuu et al., 2018) and removal of the vegetation on the boulders by sport climbers ("bouldering"; Lawyer & Haas, 2008; Blum, 2015; Antz et al., 2019).

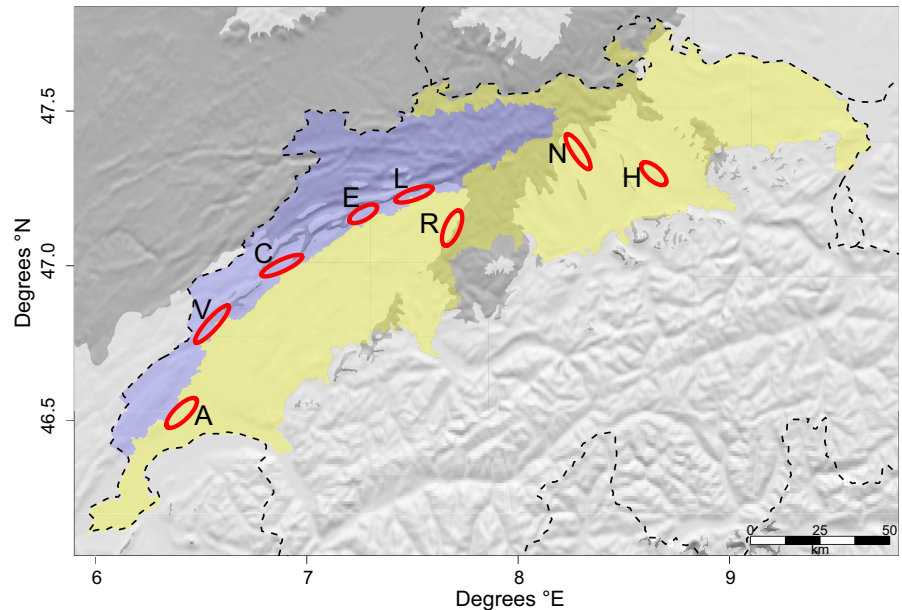
We specifically address the following three questions: (i) how are boulder size and species richness and composition related; (ii) which ecological factors drive species richness and the occurrence of boulder specialist species; and (iii) which ecological factors drive bryophyte community composition?

2 | METHODS**2.1 | Study sites and sampling**

Our study region was situated in the calcareous Swiss Plateau (molasse bedrock) and in the Jura Mountains (limestone), where Pleistocene siliceous erratic boulders originating from siliceous areas in the Alps have been deposited in large numbers (Figure 1). The study region is characterised by a mosaic of agricultural areas, forests, and residential and industrial areas in a temperate sub-oceanic climate (annual mean temperature 3.9–10.9°C, annual precipitation 970–1,890 mm, elevation 350–1,680 m a.s.l.; www.meteoschweiz.admin.ch).

Within our study region, we selected eight study areas that contain abundant siliceous erratic boulders. Four areas were distributed on the southern Jura slopes where erratic boulders had already been explored in a floristic study by Meylan (1912), and four areas were located in glacial landscapes of the Swiss Plateau that were glaciated during the Last Glacial Maximum. Each elliptical study area of 40–62 km² enclosed the regional pool of erratic boulders (Figure 1). We selected a stratified random sample of ten forest and ten non-forest

FIGURE 1 Location of the eight study areas (red ellipses; identification codes as in Table S1) on the Swiss Plateau (yellow) and in the Swiss Jura Mountains (blue; BAFU, 2006). Light grey areas of the background map were glaciated during the Last Glacial Maximum, whereas darker grey areas were ice-free (Bini et al., 2009). Dashed lines indicate national borders (Background map: Jarvis et al., 2008)



boulders per study area. Stratification was applied because the abundance of erratic boulders was about five times higher in forests than in non-forested land.

The sampling protocol is described in detail in Appendix S1. In short, we first selected the sample boulders from coordinates of erratic boulders recorded on geological maps (Appendix S2). For a selected boulder to be sampled in the field, a series of criteria had to be fulfilled. First, an erratic boulder had to be present at the selected boulder's coordinates. The above-ground dimensions (hereafter, dimensions always refer to above-ground dimensions) had to be at least 0.5 m in height and 0.5 m in length. The boulders had to be non-calcareous (i.e., no reaction with 10% HCl) and not influenced by calcareous surface water. If multiple boulders fulfilled these criteria at a coordinate point, we chose the largest boulder for sampling. If no boulder fulfilled the above criteria, we selected a replacement boulder by a predefined procedure. An overview of study areas and sampled and replaced boulders is given in Appendix S3.

2.2 | Data

For each sampled boulder, we compiled a complete list of all bryophyte species (samples are archived in Herbarium Z) and a set of numerical variables describing the boulder and its environment (Table 1). Nomenclature followed the Swiss bryophyte checklist of Meier et al. (2013), and taxonomically difficult bryophyte species groups were treated as aggregates (Appendix S4). Following Virtanen and Oksanen (2007), we defined boulder size as the boulders' surface area based on an approximation of a cuboid boulder shape. We described the vegetation structure and substrates on erratic boulders by estimating the percent cover of bryophytes, lichens, tracheophytes, litter, humus and open rock.

Meylan (1912) underlined the importance of direct solar radiation for bryophyte species composition on erratic boulders.

Accordingly, we modelled the maximum potential annual total direct radiation input at the highest point of each boulder (recorded with a differential GNSS device [Geo 7X, Trimble, Sunnyvale, USA]) based on synthetic hemispherical images generated from airborne LiDAR data (collected between 2016 and 2019) and the digital elevation model *swissAlti3D* from *swisstopo* (www.swisstopo.admin.ch), using a modified version of the method described by Webster et al. (2020).

Weibull and Rydin (2005) showed that the composition of the canopy above a boulder can influence its bryophyte community. Accordingly, we estimated the percent cover of trees, shrubs, and evergreens (i.e. evergreen conifers and evergreen broad-leaved species) above each boulder (shoot presence, in foliate state). Within a radius of 25 m of each boulder, we counted the number of additional siliceous erratic boulders and determined the percent cover of forest and buildings using the digital Topographic Landscape Model (TLM) from *swisstopo*. We calculated the Euclidean distance to the nearest building (only used in models for *Paraleucobryum longifolium*). We recorded elevation in the field while mean annual precipitation and temperature were derived from interpolated maps with 100-m resolution generated by Descombes et al. (2020) using data of Karger et al. (2017). As a proxy for air humidity, we considered the minimum Euclidean distance to the nearest river, derived from the TLM. Additionally, we characterised the boulders' ecology as their bryophytes' mean unweighted ecological indicator values (Landolt et al., 2010) for moisture (F), light (L), reaction (R), nutrients (N) and hemeroby (EM; hemeroby quantifies anthropogenic influence on site conditions).

2.3 | Analyses

We conducted data analyses in R 3.6.3 (R Core Team, 2017). Unless otherwise stated, all analyses were based on species presence/absence on the 160 sampled boulders and performed separately for all bryophytes and for the boulder specialists.

TABLE 1 Overview of the variables analysed for 160 siliceous erratic boulders in the calcareous Swiss Plateau and Jura Mountain

Variable	Range	Mean \pm SD	Unit	GLMM
Number of bryophyte species				
All species	0–36	10.6 \pm 5.4	Count	Included
Boulder specialists	0–8	1.5 \pm 1.7	Count	Included
Boulder size				
Boulder size	1.5–1,082	31.6 \pm 93.8	m ²	Included; log-transformed
Vegetation and substrates on boulder				
Bryophyte cover	0–99.8	49.9 \pm 36.6	%	
Lichen cover	0–100	22.6 \pm 31.6	%	
Tracheophyte cover	0–80	5.9 \pm 13.2	%	
Litter cover	0–95	12.1 \pm 18.4	%	
Humus cover	0–95	11.3 \pm 20.2	%	
Rock cover	0–100	21.9 \pm 26.3	%	
Radiation				
Direct radiation	28–7,907	3,652.2 \pm 2,581.3	MJ/m ² /year	Included
Canopy above boulder				
Trees above	0–100	63.7 \pm 44.1	%	Included
Shrubs above	0–100	12.6 \pm 25.2	%	Included
Evergreens above	0–100	15.9 \pm 32.1	%	Included
Surrounding of boulder				
Boulders in 25 m radius	0–26	2.0 \pm 3.5	Count	Included; square-root-transformed
Forest in 25 m radius	0–100	55.9 \pm 44.9	%	Excluded (highly correlated with radiation)
Buildings in 25 m radius	0–26	1.2 \pm 4.3	%	Included
Distance to buildings	2–695	160.0 \pm 127.2	m	Included; log-transformed (for <i>Paraleucobryum</i> models)
Climatic variables				
Elevation	382–1,262	635.9 \pm 177.2	m	Included
Precipitation	880–1,669	1,277.5 \pm 165.1	mm/year	Included
Temperature	5.9–10.6	9.3 \pm 1.0	°C	Excluded (highly correlated with elevation)
Distance to river	0.5–2,246	468.3 \pm 500.9	m	Included, log-transformed
Indicator values				
Moisture <i>F</i>	2–3.13	2.6 \pm 0.24		
Light <i>L</i>	1.67–4	2.56 \pm 0.51		
Reaction <i>R</i>	1.75–4.33	2.72 \pm 0.55		
Nutrients <i>N</i>	1–5	2.1 \pm 0.56		
Hemeroby <i>EM</i>	1.33–3.4	2.31 \pm 0.49		

Note: The last column (generalised linear mixed-effects model – GLMM) shows if and, where appropriate, how the variable was included in the generalised linear mixed-effects models.

2.3.1 | Definition of boulder specialists

We defined boulder specialists based on their substrate preferences and their reaction indicator value *R*, retrieved from Landolt et al. (2010) and Hill et al. (2007), which together covered all species identified in this study except *Sciuro-hypnum flotowianum*. We filtered our species list for species with rock as primary substrate and acidophile habitat preferences indicated by $R \leq 2$ for the five-level indicator values of Landolt et al. (2010) or $R \leq 4$ for the ten-level indicator values of Hill et al. (2007).

2.3.2 | Species–area relationships, SLOSS and nestedness

We assessed the effect of boulder size (*A*) on the species richness (*S*) of an individual boulder by fitting the power function $S = c \times A^z$ using non-linear regression (Ritz & Streibig, 2008). This power function has been shown to be the most adequate function for describing species–area relationships (Dengler, 2009). Mathematically, the fitted parameter *c* reflects the expected mean number of species per unit area (in our case one square metre), and the parameter *z*

reflects the rate of change in species richness in response to area (Fattorini et al., 2017). Higher z -values are expected for islands than for mainland because the probability of extinction for a given species is high on a small island while the corresponding probability of colonisation is low, whereas larger islands approach the low extinction rates and high colonisation rates in a given area of mainland (MacArthur & Wilson, 1967). Hence, we expected higher z -values for boulder specialists, for which boulders are actual habitat islands, than for species that also occur in the landscape matrix around boulders (Dembicz et al., 2020).

To elucidate the importance of boulder size for total species richness, we calculated cumulative species–area curves, as proposed by Quinn and Harrison (1988), to determine if single large or several small islands (SLOSS) harbour more species (Fahrig, 2020), using the package *Lexiguel* (Alvarez, 2020). This approach is based on cumulative species–area curves with the cumulative area of islands (or any other habitat patches) along the X -axis and the cumulative number of species along the Y -axis. The islands are ranked by their size, once in ascending and once in descending order, which results in two curves. By comparing the two curves, one can determine whether several small islands harbour more species than a few large islands of the same total area. This is the case if the ascending curve lies above the descending curve, which results in a value >1 for the SLOSS index, which is the quotient of the areas under the ascending and the descending curve (Quinn & Harrison, 1988).

In order to check if the species composition of small boulders was nested within the species composition of large boulders, we calculated the NODF metric (nestedness based on overlap and decreasing fill; Almeida-Neto et al., 2008) using the functions provided in the package *vegan* (Oksanen et al., 2019). In a sorted presence/absence matrix – in our case decreasingly sorted by boulder size and species frequency – the NODF metric (ranging from 0 to 100) quantifies the extent to which row and column sums decrease from left to right and top to bottom. In a perfectly nested matrix all species on smaller boulders would also be present on all larger boulders, which corresponds to a matrix with all presences in the upper left triangle of the matrix and a NODF of 100. The significance of NODF values was tested against the values retrieved from 999 permuted matrices using the "c0" method that preserves species frequencies.

2.3.3 | Analyses of species richness and occurrence of specialist species

In order to identify variables that explain variation in species richness and species occurrence on erratic boulders, we applied multi-model inference of generalised linear mixed-effects models (GLMMs; Burnham & Anderson, 2002; Bolker et al., 2009) as implemented in Kiebach et al. (2017). Note that the term “explain” is used here in a strictly statistical sense, i.e., for the variation in a response variable accounted for by a set of predictors. As predictors we used a subset of the environmental variables described above (see Table 1). Because the predictor pairs temperature and elevation, and forest cover and

direct radiation, respectively, were highly correlated ($|\text{Spearman's } \rho| > 0.7$), temperature and forest cover were excluded from the analyses. We included study area as a random factor. In order to improve model convergence, fit and interpretation, selected predictors were transformed (Table 1). All predictors were standardised to mean = 0 and standard deviation = 0.5 (Schielzeth, 2010). We constructed GLMMs using the package *lme4* (Bates et al., 2015). To analyse species richness we conducted Poisson regression by specifying a Poisson error structure and the log-link function. To analyse individual boulder specialist species, we conducted logistic regression by specifying a binomial error structure and the logit-link function. Thereby, we only analysed boulder specialists that occurred on at least 10% of the sampled boulders, namely *Grimmia hartmanii*, *Grimmia trichophylla*, *Hedwigia ciliata* and *Paraleucobryum longifolium*. For all 27 occurrences of *Paraleucobryum longifolium* the predictor “buildings” had a value of zero, which did not allow a meaningful estimate of the regression parameters by the GLMMs. Therefore, for *Paraleucobryum longifolium* we used the minimum Euclidean distance to the nearest building as a predictor for “buildings.” All full models were checked for overdispersion using the package *blmeo* (Korner-Nievergelt et al., 2015). No signs of overdispersion were found. We conducted model simplification, selection and averaging with functions implemented in the package *MuMIn* (Barton, 2015). For each full model, we generated sub-models with all possible predictor combinations and extracted the relative variable importance (RVI) of the predictors. Then, we retained all models with $\Delta\text{AIC} < 2$ relative to the best model, averaged the models, and generated average parameter estimates for the predictors.

2.3.4 | Analyses of community composition

In order to identify environmental variables that correlate with species composition on erratic boulders, we conducted a detrended correspondence analysis (DCA; Hill, 1979; Hill & Gauch, 1980) and calculated correlation coefficients (Spearman's ρ) between axis positions and environmental variables (Table 1). This analysis was based on the species data filtered for species with more than one occurrence and boulders harbouring more than three species (resulting in a data set of 101 species and 151 boulders), using the functions provided in the package *vegan* (Oksanen et al., 2019). For corroboration of the DCA results we performed a parallel ordination (van Son et al., 2014) by which the same data were subjected to (global) non-metric multi-dimensional scaling (NMDS; Appendices S5 and S6). The two NMDS axes were highly correlated with the corresponding DCA axes (Spearman's ρ of -0.96 for axis 1 and 0.81 for axis 2, respectively; Liu et al. 2008).

For visualisation and interpretation of the DCA ordination, we fitted vectors for variables that were at least moderately correlated ($|\text{Spearman's } \rho| > 0.5$) with one of the two first DCA axes to the ordination diagram, using the *envfit* function of *vegan* (Oksanen et al., 2019). The results indicated separation of boulder specialists along the vector for direct radiation fitted to the two-dimensional ordination diagram. We explored this relationship further using

boxplots of occurrences of all boulder specialists along the radiation gradient.

Additionally, we classified bryophyte communities with *k*-means non-hierarchical clustering (Borcard et al., 2018). Based on silhouette plots (package *cluster*; Maechler et al., 2019) for different numbers of clusters, we chose four clusters. We further characterised clusters identified by *k*-means clustering by indicator species (Appendix S7) and boxplots for the environmental variables (Appendix S8).

3 | RESULTS

3.1 | Diversity of boulders and species

In total we visited 321 coordinates with erratic boulders, 101 of which were replaced because the boulder(s) at the given coordinates did not fulfil our criteria, and 60 were replaced because no boulder was present. The surface area of the sampled boulders covered three orders of magnitude (Table 1). On the 160 boulders studied, we recorded a total of 138 bryophyte species (Appendix S9), 19 of which we identified as boulder specialists (Table 2). These largely corresponded to the boulder specialists listed for the Jura Mountains by Meylan (1912). Species richness per boulder ranged from 0 to 36 and boulder specialist richness ranged from 0 to 8 (Table 1). On 61% of the sampled boulders we found at least one boulder specialist.

3.2 | Species–area relationships, SLOSS and nestedness

The *z*-values obtained by fitting a power function to the species–area data (Figure 2) indicated that boulder size had a stronger influence on the number of boulder specialists ($z = 0.40$; 0.34–0.47, 95% confidence interval) than on total species richness ($z = 0.21$; 0.17–0.25). The largest boulder was an outlier in terms of size (Figure 2). However, when we removed this boulder from the analyses (Appendix S10) the estimated *z*-values ($z = 0.42$ for boulder specialist richness, $z = 0.18$ for total species richness) remained within the confidence intervals of the estimates for the complete data set.

SLOSS analyses indicated that several small boulders harboured more species than one or a few large boulders of the same surface area (Figure 3). This relationship was more accentuated when all species were considered (SLOSS index 2.03) than for boulder specialists only (SLOSS index 1.54).

Analyses of nestedness revealed that species present on small boulders were significantly nested within the species present on larger boulders. Nestedness was more accentuated for boulder specialists (NODF = 37.5, mean simulated NODF = 19.4, $p < 0.001$) than for total species richness (NODF = 19.1, mean simulated NODF = 12.5, $p < 0.001$; incidence plots in Appendix S11).

3.3 | Species richness and occurrence of specialist species

Boulder size contributed highly significantly, positively, to all averaged generalised linear mixed-effects models (Table 3, Table S5). Direct radiation was only significant in some single-species models, with positive as well as negative coefficients. Thus the probability of *Hedwigia ciliata* presence on an erratic boulder increased with increasing direct radiation, while the probability of *Paraleucobryum longifolium* and *Grimmia hartmanii* presence decreased. No significant effects were found for the presence of additional erratic boulders within a 25-m radius. The percentage of area covered by buildings within a 25-m radius had a negative effect on the number of boulder specialists and on the presence of *Grimmia hartmanii* and *Hedwigia ciliata*. For *Paraleucobryum longifolium*, distance to the nearest building showed a marginally significant positive effect. The percent cover of tree canopy above a boulder had a significant positive effect on *Grimmia hartmanii* presence while the percent cover of shrubs had a significant positive effect on total species richness. The percent cover of evergreens showed a marginally significant negative effect on *Grimmia trichophylla* presence. Elevation positively affected the number of boulder specialists, as well as *Grimmia hartmanii* and *Paraleucobryum longifolium* presence. The two predictors “precipitation” and “distance to the nearest river” were not significant in any model.

TABLE 2 The 19 boulder specialists (acidophilic rock-dwelling bryophyte species) found on 160 siliceous erratic boulders in the calcareous Swiss Plateau and Jura Mountains

<i>Dicranoweisia crispula</i> (1; LC)	<i>Grimmia longirostris</i> (3; LC)	<i>Hedwigia stellata</i> (2; VU)
<i>Dicranum fulvum</i> (12; LC)	<i>Grimmia muehlenbeckii</i> (1; LC)	<i>Orthotrichum rupestre</i> (14; LC)
<i>Grimmia decipiens</i> (3; VU)	<i>Grimmia ovalis</i> (11; NE)	<i>Paraleucobryum longifolium</i> (27; LC)
<i>Grimmia elatior</i> (5; LC)	<i>Grimmia ramondii</i> (1; LC)	<i>Racomitrium aciculare</i> (1; LC)
<i>Grimmia hartmanii</i> (67; LC)	<i>Grimmia trichophylla</i> (25; NT)	<i>Racomitrium heterostichum</i> aggr. (4; NE)
<i>Grimmia laevigata</i> (7; LC)	<i>Hedwigia ciliata</i> (48; LC)	<i>Racomitrium microcarpon</i> (1; VU)
		<i>Ulota hutchinsiae</i> (2; VU)

Note: The species' frequency in this study (number of boulders) and Swiss national red list status (LC: least concern; NE: not evaluated; NT: near threatened; VU: vulnerable – Schnyder et al., 2004) are given in parentheses.

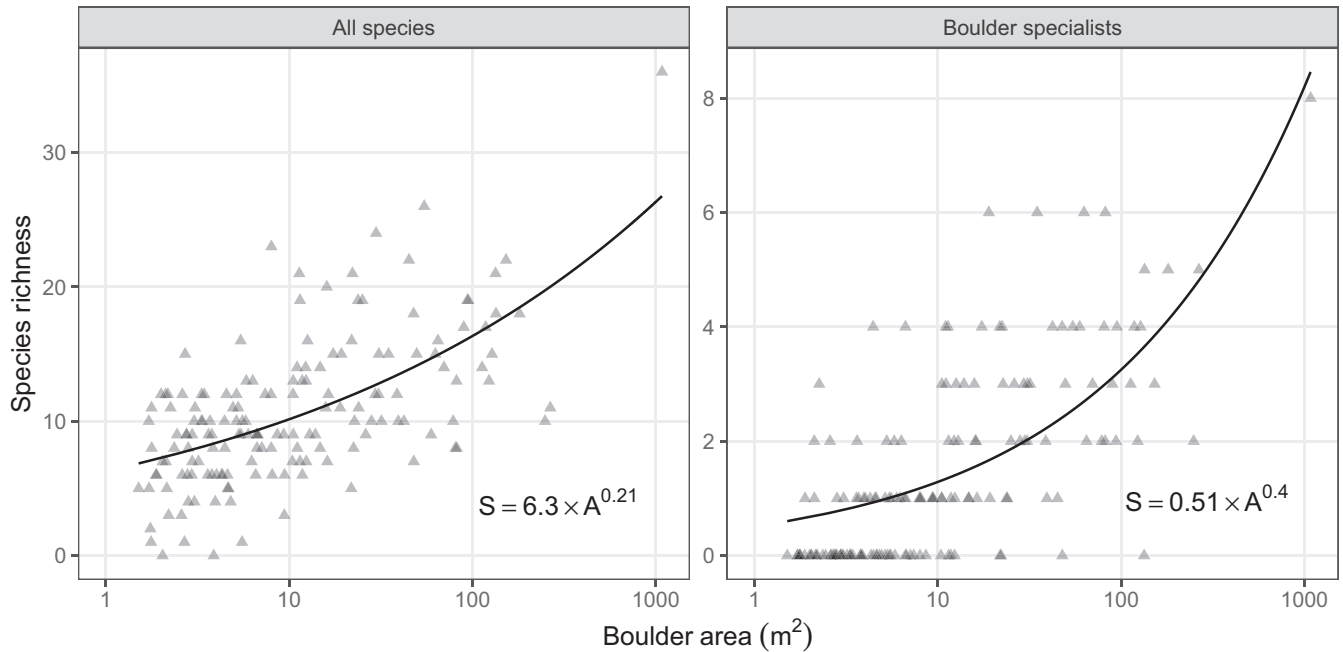


FIGURE 2 Species (S)–area (A) relationships of bryophytes on 160 siliceous erratic boulders, (a) for total species richness and (b) for species richness of boulder specialists (note that the Y-axis scale differs between panels, and that the X-axis scale is logarithmic). The regression lines are power functions fitted with non-linear regression

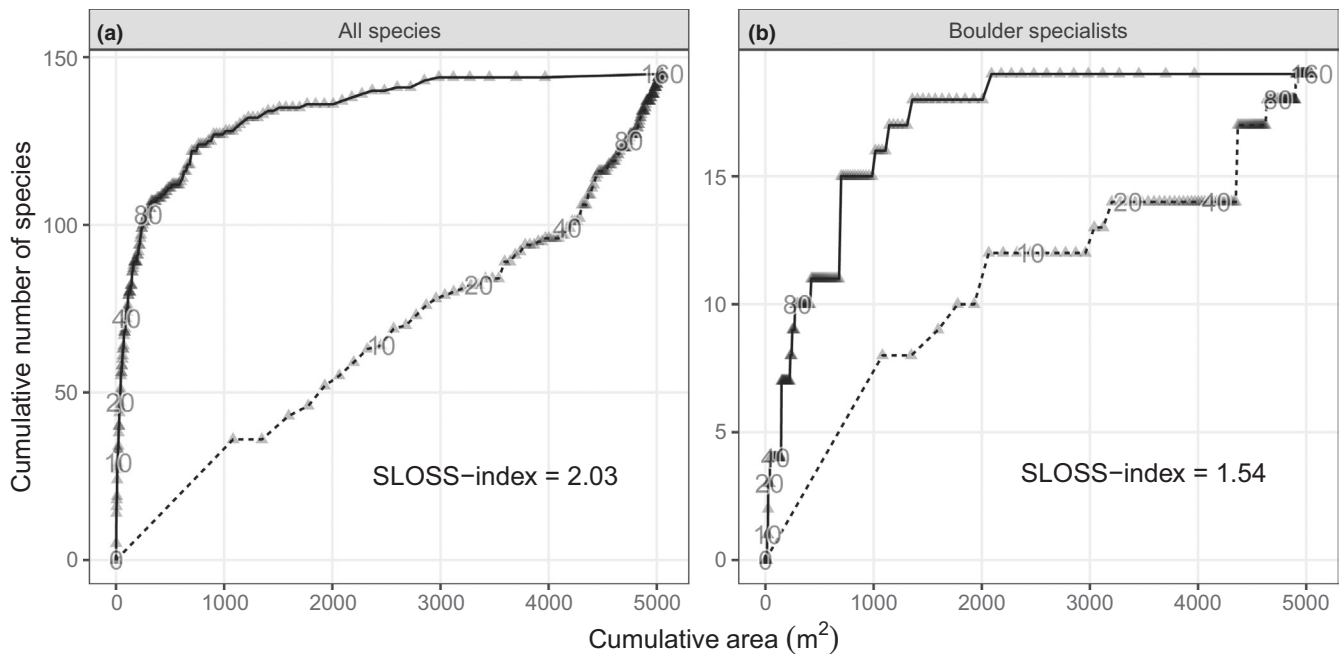


FIGURE 3 Cumulative species–area curves of bryophytes on siliceous erratic boulders sorted by surface area in ascending (solid curve) and descending order (dashed curve) (a) for all species and (b) for boulder specialists (note that the Y-axis scale differs between panels). Grey numbers indicate the number of boulders involved at given points on the curves. The SLOSS index is the quotient of the areas below the two curves

3.4 | Community composition

Multiple significant, moderate to strong correlations (Spearman's $\rho > 0.5$) between environmental variables and each of the first two DCA axes (eigenvalues 0.55 and 0.34, gradient lengths 4.74 and

3.81 for axis 1 and axis 2, respectively), revealed potential drivers of community composition of the studied erratic boulders. The main gradient along the first axis corresponded to the bipartition into forest vs open-land communities, as the variables associated with forest conditions – percentage of forest around boulders, percentage

TABLE 3 Results of generalised linear mixed-effects models (GLMMs) fitted to species numbers with Poisson regression and to the occurrence of four boulder specialist species with logistic regression

Predictor	All species			Boulder specialists			Grimmia hartmanii			Grimmia trichophylla			Hedwigia ciliata			Paraleucobryum longifolium		
	Est.	p	RVI	Est.	p	RVI	Est.	p	RVI	Est.	p	RVI	Est.	p	RVI	Est.	p	RVI
Boulder size	0.64	<0.001	1.00	1.29	<0.001	1.00	3.05	<0.001	1.00	2.15	<0.001	1.00	2.84	<0.001	1.00	2.20	<0.001	1.00
Direct radiation	-0.06	0.243	0.38	-0.18	0.309	0.34	-1.05	0.050	0.73	n	0.26	0.26	1.57	0.003	0.94	-2.00	0.006	0.95
Boulders	-0.04	0.454	0.31	-0.08	0.536	0.29	n	0.26	0.26	0.33	0.496	0.28	-0.25	0.575	0.27	n	n	0.26
Buildings	-0.09	0.105	0.57	-1.03	0.004	1.00	-1.16	0.129	0.68	-0.63	0.439	0.36	-2.57	0.031	0.99	1.37 ^a	0.058	0.73
Trees above	0.03	0.583	0.30	-0.22	0.15	0.52	1.43	0.018	0.91	-0.43	0.376	0.36	-0.37	0.483	0.32	n	n	0.29
Shrubs above	0.18	<0.001	1.00	-0.07	0.669	0.28	n	0.27	0.27	n	0.25	0.25	-0.28	0.613	0.28	0.643	0.282	0.35
Evergreens above	-0.06	0.314	0.36	-0.25	0.140	0.50	0.38	0.362	0.35	-3.94	0.082	0.96	-0.78	0.226	0.43	n	n	0.27
Elevation	-0.06	0.419	0.28	0.37	0.004	0.91	1.99	<0.001	1.00	0.41	0.353	0.29	-0.45	0.384	0.32	1.99	<0.001	0.99
Precipitation	-0.06	0.381	0.30	0.15	0.370	0.35	-0.26	0.561	0.27	-0.23	0.673	0.28	n	n	0.26	n	n	0.25
Distance to river	-0.09	0.159	0.45	-0.20	0.253	0.36	0.61	0.211	0.41	0.96	0.124	0.53	-0.74	0.170	0.43	0.382	0.563	0.29

Note: Estimates (Est.) are standardised coefficient estimates after model averaging of the best candidate models (n: predictor not included in the best models), whose p-values are given (in bold: $p < 0.1$). Relative variable importance (RVI) is the sum of Akaike weights over all possible candidate models containing the predictor.

^aFor *Paraleucobryum longifolium* the predictor "buildings" corresponds to the minimum Euclidean distance to the next building (see text).

of evergreens above boulder, litter and humus cover, bryophyte cover and the moisture indicator value F – correlated negatively with the first axis, whereas the amount of direct radiation, lichen cover and the indicator values for light, hemeroby and reaction correlated positively with this axis (Figure 4, Table 4). Along the second axis, a negative correlation with the number of boulder specialists indicated separation of communities containing specialist species from communities lacking specialist species. This accorded with the positive correlation of this axes with the indicator value for reaction. Projection of the k -means clusters (Appendices S5, S6) on the DCA ordination diagram (Figure 4) substantiated the separation into two forest communities (c3 and c4) and two open-land communities (c1 and c2) which differ by the presence (c2 and c3) and absence (c1 and c4) of boulder specialist species.

3.5 | Radiation gradient

Boulder specialists occurred across the whole range of direct radiation present in the data set, but the individual species showed differences in their preferences and amplitudes for direct radiation (Figure 5). Forest boulders generally had lower radiation values than non-forest boulders. Two specialist species were exclusively found on boulders in forests, and seven specialists were exclusively found on boulders outside forests.

4 | DISCUSSION

Our most important findings were that boulder specialists had a steeper species-area curve than the total number of species present on boulders, which underlines the island properties of boulders for specialist species (Figure 2) and suggests that species richness is mainly driven by boulder size (Table 3) while community composition is mainly structured by the distinction between forest and open-land boulders (Figure 4, Table 4).

4.1 | Diversity of boulders and bryophyte species

The current distribution of erratic boulders in Switzerland is mainly shaped by their massive depletion due to agricultural land clearance (Akçar et al., 2011). This pattern is also evident in our study areas, where 82% of the erratic boulders for which coordinates were available were situated in forests (Appendix S3). Ongoing destruction of erratic boulders in open land may explain why 24% of boulders in the non-forest stratum were not found at the original coordinates, compared with only 10% for boulders in forests (Appendix S3).

Considering the small total habitat area sampled here (5,000 m²; Figure 3), the 19 specialist species found in our study, four of which are threatened (Table 2), can be considered a major contribution to biodiversity at the landscape level. Including the seven additional boulder specialist bryophytes reported by Meylan (1912), three of

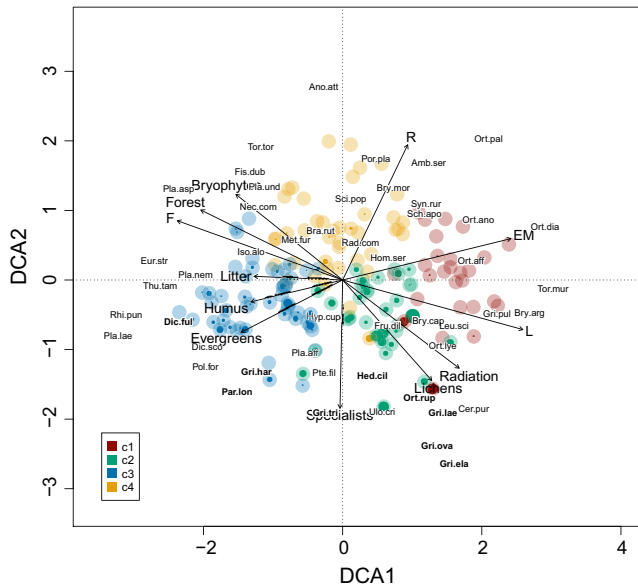


FIGURE 4 Detrended correspondence analysis (DCA) of bryophyte species composition on 151 siliceous erratic boulders. Circles represent individual boulders, with the colour indicating their assignment to k -means clusters (Appendices S7, S6). The size of the filled part of the circles is proportional to the number of boulder specialists on the erratic boulders (minimum: 0; maximum: 8). Boulder specialists with more than five occurrences are given in bold, and non-specialist species with more than 10 occurrences are given in normal font. Arrows indicate the direction and relative strength (length) of linear correlations with variables which at least moderately correlated ($|\text{Spearman's } \rho| > 0.5$) with one of the first two DCA axes (see Table 4)

which are currently threatened (Schnyder et al., 2004), and additional boulder specialist species that have not yet been recorded in the study region but could potentially occur there (e.g. further species of the genus *Grimmia*; Hepenstrick, 2021), the total number of boulder specialist bryophytes present on the Swiss Plateau and in the Jura Mountains may be around 30 species, underlining the biological conservation value of erratic boulders in this region.

4.2 | Boulder size and species richness

In agreement with Weibull and Rydin (2005) and Virtanen and Oksanen (2007), we confirmed a positive species–area relationships on erratic boulders. This finding is not surprising, considering that the size of the sampled boulders spanned three orders of magnitude and the ubiquity of positive species–area relationships in ecology (Drakare et al., 2006). The comparably steep slope of our species–area curve for specialist bryophyte species of siliceous erratic boulders (Figure 2), corresponding to a z -value of 0.40, matches well with the z -value of 0.39 for bryophyte and lichen species restricted to calcareous erratic boulders in Finland, as reported by Virtanen and Oksanen (2007). While the Finnish study ignored species also occurring in the matrix around boulders, we compared boulder specialist species richness to total species richness, for which we found a

distinctively lower z -value of 0.21. This pattern agrees with island biogeography theory (MacArthur & Wilson, 1967), as it underlines the island-like properties of erratic boulders for specialist species: the colonisation and extinction of specialist species are more strongly influenced by the size of their special habitat island than the colonisation and extinction of species that also occur in the matrix, which results in a steeper species–area curve for island specialists. This pattern of higher z -values for habitat specialists in habitat islands was also found by Dembiczy et al. (2020) for vascular plant species in insular steppe fragments, reporting $z = 0.32$ for total species richness and $z = 0.43$ for specialist species of steppes.

SLOSS analysis shows that several small boulders harbour more species than a single large boulder or few large boulders adding up to the same surface area (i.e. $SL < SS$; Figure 3). This result contrasts the original theory ($SL > SS$; Diamond, 1975), but it agrees with most empirical studies conducted to explore this relationship (reviewed by Fahrig, 2020). In our case, we explain the observed relationship of $SL < SS$ with the pronounced ecological and floristic gradients among the sampled boulders (Figure 4) which, most likely, exceed the maximum variation in species composition found on one single large boulder. In other words, for erratic boulders, a set of several small patches is environmentally more heterogeneous than a one single large patch (cf. Fahrig, 2020).

Analysis of nestedness showed that the species composition of small boulders made up a nested subset of the total species composition of larger boulders. Hence, no common species in our data set occurred exclusively on small boulders. Additionally, we found stronger nestedness for specialist species (NODF = 37.5) than for all species (NODF = 19.5). This result suggests that habitats are nested (Ulrich et al., 2009): the larger a boulder is, the more likely it is that the boulder contains well-lit patches that favour occurrences of heliophilous boulder specialist species in addition to shade-adapted specialist species that may find habitat on the shaded north face of large boulders (Figure 5).

4.3 | Species richness and occurrence of specialist species

In accordance with our univariate analysis of boulder size (Figure 2), boulder size was the most important predictor, positively related to species richness in GLMM analyses (Table 3). The other environmental predictors, however, showed different and often inconsistent relationships with total species richness, specialist species richness and single species. Such diverse responses were also reported by Kiebacher et al. (2017) for bryophytes on island-like trees in pastures.

Besides boulder size, the only variable related to total species richness was shrub cover. This positive relationship with species richness may be due to a microclimatic balancing effect of the shrub leaf canopy on the otherwise rather extreme rock microclimate (Larson et al., 2000), enabling the growth of a wider variety of species on boulders, including epiphytic species (e.g. *Orthotrichum* spp.).

Variable	DCA1		DCA2	
	rho	p	rho	p
Number of bryophyte species				
All species	0.083	0.309	0.070	0.391
Boulder specialists	-0.205	0.012	<u>-0.646</u>	<u><0.001</u>
Boulder size				
Boulder size	-0.065	0.428	-0.470	<0.001
Vegetation and substrates on boulder				
Bryophyte cover	-0.590	<0.001	0.233	0.004
Lichen cover	<u>0.615</u>	<0.001	-0.264	0.001
Tracheophyte cover	-0.132	0.107	-0.072	0.377
Litter cover	<u>-0.530</u>	<0.001	0.091	0.267
Humus cover	<u>-0.524</u>	<0.001	-0.038	0.643
Rock cover	0.289	<0.001	0.126	0.122
Radiation				
Direct radiation	<u>0.629</u>	<0.001	-0.261	0.001
Canopy above boulder				
Trees above	-0.332	<0.001	0.429	<0.001
Shrubs above	0.018	0.826	0.310	<0.001
Evergreens above	<u>-0.639</u>	<0.001	-0.078	0.344
Surrounding of boulder				
Boulders in 25 m radius	-0.254	0.002	0.048	0.559
Forest in 25 m radius	<u>-0.729</u>	<0.001	0.106	0.194
Buildings in 25 m radius	0.405	<0.001	0.035	0.669
Distance to buildings	-0.440	<0.001	-0.03	0.714
Climatic variables				
Elevation	-0.062	0.450	-0.284	<0.001
Precipitation	-0.002	0.976	-0.251	0.002
Temperature	0.157	0.054	0.357	<0.001
Distance to river	0.058	0.479	-0.197	0.016
Indicator values				
Moisture <i>F</i>	<u>-0.808</u>	<0.001	0.160	0.050
Light <i>L</i>	<u>0.892</u>	<0.001	-0.059	0.472
Reaction <i>R</i>	<u>0.504</u>	<0.001	<u>0.558</u>	<0.001
Nutrients <i>N</i>	0.448	<0.001	0.198	0.015
Hemeroby <i>EM</i>	<u>0.819</u>	<0.001	0.221	0.006

Note: Significant ($p < 0.05$) correlations are marked bold and moderate to stronger correlations ($|\text{Spearman's rho}| > 0.5$) are underlined.

Boulder specialist species richness was negatively related to the occurrence of nearby buildings and positively related to elevation. The negative relationship with nearby buildings may be due to frequent human disturbance such as excavation of boulders during development of infrastructure of all kinds, cleaning of boulders in gardens, etc., which may impede the growth of bryophytes (Wächter, 1996). The positive relationship with elevation on specialist species may be caused by different aspects of this multi-faceted predictor that correlates with, e.g., temperature, deposition of atmospheric pollutants (Lovett & Kinsman, 1990) and land use intensity (Körner, 2007).

In agreement with the results obtained for boulder specialist richness, three of the four single species tested showed a negative relationship to buildings and three species showed a positive relationship to elevation. *Hedwigia ciliata* was the only species with a negative, but statistically not significant relationship to elevation. This may reflect the thermophilic preference of this species. Boulder specialist species did not display consistent relationships with other variables, reflecting their different environmental niches (Nebel & Philippi, 2000). The typical forest species *Grimmia hartmanii* and *Paraleucobryum longifolium* were negatively related to direct

TABLE 4 Table of correlations (Spearman's rho) between the analysed variables (Table 1) and the two DCA axes

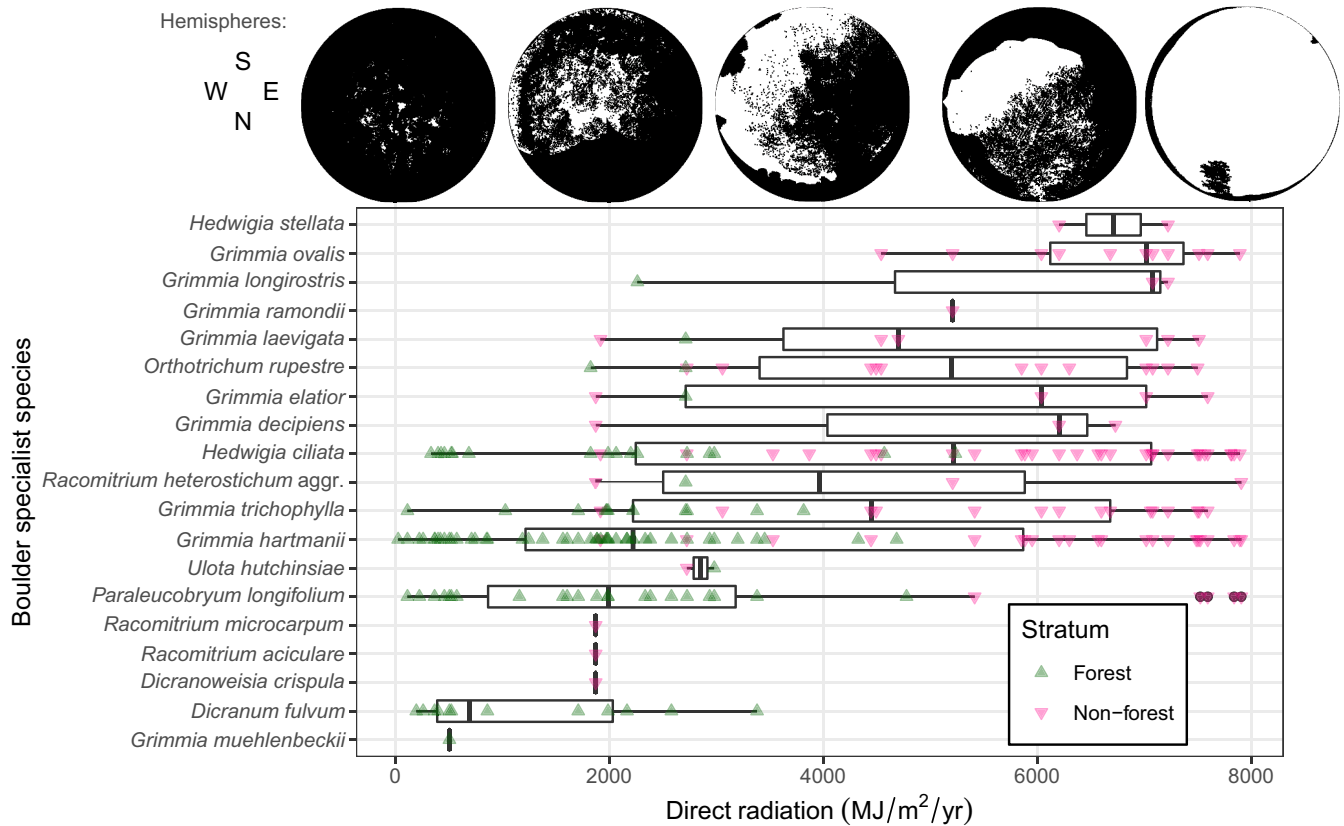


FIGURE 5 Boxplots for the potential annual direct radiation for erratic boulders on which boulder specialist species were recorded. Triangles depict occurrences along the radiation gradient and their colours indicate whether the corresponding boulder was located in the forest or the non-forest stratum. The images above the plots are examples of the synthetic hemispherical images from which the radiation values were derived

radiation, while *Hedwigia ciliata* showed a positive response. The positive relationship with tree cover found for *Grimmia hartmanii* is in line with the findings of Weibull (2001), who stated that this species thrives on boulders influenced by rain throughfall and deciduous litter. While Weibull and Rydin (2005) found reduced species richness on boulders under evergreen trees (*Picea abies*), our analyses only show a marginally significant negative relationship with the cover of evergreen trees in *Grimmia trichophylla*. It should be noted that we did not allow for non-linear relationships in the GLMM analyses. As species do not respond linearly but rather unimodally to long environmental gradients, the linear approximations of our analyses rather point towards the species optimum which may lay towards the end or beyond the assessed environmental gradient. Unimodal responses with maxima near the centre of an assessed environmental gradient could not be detected by our analyses (Halvorsen, 2012).

Given the pronounced positive relationship with boulder size, the absence of a significant, positive relationship with the presence of nearby erratic boulders is surprising and in contrast to the results of Virtanen and Oksanen (2007), who found a positive effect of connectivity among boulders on species richness in their study area, in which they sampled every single boulder. However, our sampling design may not be optimal for analysis of connectivity among boulders; the fact that we sampled the largest boulder in cases where multiple boulders were present further reduced the chance of detecting a

connectivity effect that might have been detectable if nearby boulders had been investigated.

The two predictors that were included to describe water availability, i.e. precipitation and distance to the nearest river, did not show significant relationships with any response variable, even though the moisture indicator values suggested existence of a humidity gradient in our data set (Figure 4). Consequently, we conclude that the site-specific microclimatic influence on humidity, governed by local radiation and canopy cover, is more important for the bryophyte species composition on erratic boulders than the more regional predictors precipitation and distance to the nearest river.

4.4 | Community composition

The major ecological and floristic bipartition into forest boulders with high bryophyte cover and open-land boulders with high lichen cover (Figure 4) agrees with the original description of the typical bryophyte communities of siliceous erratic boulders in the Jura Mountains by Meylan (1912). While Meylan (1912) did not further split forest and open-land bryophyte communities on erratic boulders, we found an additional bipartition of both groups into communities that differed in the presence or absence of boulder specialists (Figure 4). In short, clusters c2 and

c3 corresponded to communities of sunny (c2) and shaded (c3) siliceous rock that were already described by Meylan (1912), while cluster c1 rather corresponded to communities of sunny mortar walls and cluster c4 rather corresponded to communities of base-rich bark (Figure 4; Mucina et al., 2016; Appendix 7). Hence, c2 and c3 represent the actual insular specialist communities on siliceous erratic boulders in calcareous areas, while c1 and c4 comprise communities typical for the landscape matrix around the boulders. This split into specialist and non-specialist communities was clearly expressed by the second DCA axis (Figure 4), which most strongly correlated with the number of boulder specialists and the mean indicator value for reaction (Table 4). Weibull and Rydin (2005) showed for erratic boulders in forests that litter pH and litter decomposability of the tree species above siliceous erratic boulders strongly influenced the boulders' community composition, which certainly also shapes bryophyte communities in our study (indicated by the significant influences of the cover of evergreens above boulders; Tables 3, 4, Figure 4). However, Weibull and Rydin (2005) did not report on a pattern that readily explains absence of boulder specialists. In contrast, they reported diverse responses of boulder specialist species to litter pH; for example, *Hedwigia ciliata* was less abundant below trees with high litter pH, whereas the opposite pattern was observed for *Grimmia hartmanii*. For the open-land community lacking specialist species (c1), we presume that anthropogenic disturbance may be the main driver that shapes this community. This is supported by the strong correlation of the hemeroby indicator value with the first DCA axis, which also separated cluster c1 from all other clusters (Figure 4, Table 4) and by our GLMM analyses that showed a negative influence of nearby buildings on specialist species richness (Table 3). Similar results were also reported by Wächter (1996), who found that anthropogenically disturbed siliceous erratic boulders in settlements harboured calciphilous bryophytes communities (maybe promoted by calcareous dust) but no boulder specialists. The boulder community in forests lacking specialist species (c4) may also result from disturbances, as suggested by Meylan (1912) who observed that boulders in recently clear-cut forests then stocked with young trees lost their boulder specialists and eventually only harboured ubiquitous species. Additionally, the fact that this cluster had the smallest mean boulder size (Appendix 8) supports the idea that larger boulders are more likely to provide favourable sites for erratic boulder specialist species (MacArthur & Wilson, 1967).

4.5 | Implications for conservation

Conservation of bryophytes is most efficient through conservation of their habitats (Hallingbäck & Hodgetts, 2000). In our study we found that large boulders were more likely to harbour more boulder specialists than small boulders (Figure 2) and that the species present on small boulders were nested in the species composition of larger boulders. Both results underline the importance

of large boulders. However, the presence of nestedness does not mean that small boulders are irrelevant for specialist species. This is exemplified by *Grimmia ramondii*, the only record of which in our study was on a small boulder that also harboured three other boulder specialist bryophytes. In fact, we also showed that, at the landscape level, many small boulders contributed more specialist species than a single or a few large boulders (Figure 3). Nevertheless, our results indicate that prioritising large boulders in conservation management efficiently maximises the number of species covered with a minimal number of boulders. Large boulders are also often protected as geosites (Gonggrijp, 2000; Reynard, 2004), facilitating the protection of their vegetation. However, the vegetation on larger boulders is more prone to deliberate anthropogenic disturbances, such as the removal of vegetation for sport climbing (Blum, 2015).

In our study area, erratic boulders were about five times less abundant outside of forests than within forests (Table S1), while boulder specialist communities in open land harboured different and more specialist species than boulder specialist communities in forests (Table 4; Figure 5). Hence, from the above findings we conclude that large, open-land erratic boulders should be prioritised for direct conservation measures. However, small boulders in the open land should not be neglected, because they may be particularly prone to complete destruction, for example due to agricultural land clearance. Conserving the contribution of small boulders to total boulder specialist diversity may be best achieved by raising the general awareness of the biological conservation value of erratic boulders amongst stakeholders in forestry, agriculture and nature conservation. For this, large boulders, well known to the public, may act as flagships.

Erratic boulders are not only witnesses of the Ice Ages (Reynard, 2004; Akçar et al., 2011) our study also highlights the boulders' biological value, i.e. their function as habitat for specialised bryophytes. Other studies showed that the same holds true for other cryptogams such as lichens (Krawiec, 1938; Epard et al., 2020) and ferns (Mazenauer et al., 2014). Considering the vast areas which have experienced Pleistocene glaciations (Ehlers & Gibbard, 2007), erratic boulders are a global phenomenon and contribute to regional biodiversity. The conclusions of our study may thus apply to erratic boulders elsewhere and to the conservation of insular rock-dwelling cryptogam communities in general.

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AUTHOR CONTRIBUTIONS

DH, AB and RH developed the design of the study. DH performed data collection and analysis and wrote the manuscript. AB and RH provided comments on the manuscript. CG contributed the variables

“forest,” “buildings” and “distance to river.” CW contributed the radiation data. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data sets generated and analysed in this study will be available on Dryad: <https://doi.org/10.5061/dryad.r4xgd2c6>.

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REFERENCES

- Akçar, N., Ivy-Ochs, S., Kubik, P.W. & Schlüchter, C. (2011) Post-depositional impacts on ‘Findlinge’ (erratic boulders) and their implications for surface-exposure dating. *Swiss Journal of Geosciences*, 104, 445–453. <https://doi.org/10.1007/s00015-011-0088-7>
- Alahuhta, J., Toivanen, M. & Hjort, J. (2020) Geodiversity–biodiversity relationship needs more empirical evidence. *Nature Ecology & Evolution*, 4, 2–3. <https://doi.org/10.1038/s41559-019-1051-7>
- Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D. & Ulrich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117, 1227–1239. <https://doi.org/10.1111/j.0030-1299.2008.16644.x>
- Alvarez, M. (2020) *R package lexiguel: miscellaneous functions*. v.0.1.0., <https://github.com/kamapu/lexiguel>
- Antz, W., Trachsel, P. & Schmid, R. (2019) *Bimano, smartphone app*. v.2.2. Ittingen: bimano GmbH.
- BAFU, & (2006) *Die biogeographischen Regionen der Schweiz (CH)*. Bundesamt für Umwelt, Bern.
- Bartoń, K. (2015) *Package ‘MuMIn’*. v.1.43.4., <https://cran.r-project.org/web/packages/MuMIn>
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bini, A., Buoncristiani, J.F., Couterrand, S., Ellwanger, D., Felber, M., Florineth, D. et al. (2009) *Die Schweiz während des letzteiszeitlichen Maximums (LGM), Karte 1: 500 000*. Wabern: Bundesamt für Landestopographie.
- Blum, C. (2015) *Steinhof - Steineberg Klettern, Familienklettern*. Basel: Topo.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. et al. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Borcard, D., Gillet, F. & Legendre, P. (2018) *Numerical ecology with R*. Berlin: Springer.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer.
- Colpa, J.G. & van Zanten, B.O. (2006) Mossen op de Nederlandse hunebedden in 2004/2005. *Buxbaumiella*, 75, 34–50.
- Dembicz, I., Moysiyenko, I.I., Kozub, Ł., Dengler, J., Zakharova, M. & Sudnik-Wójcikowska, B. (2020) Steppe islands in a sea of fields: where island biogeography meets the reality of a severely transformed landscape. *Journal of Vegetation Science*, 32, e12930. <https://doi.org/10.1111/jvs.12930>
- Dengler, J. (2009) Which function describes the species–area relationship best? A review and empirical evaluation. *Journal of Biogeography*, 36, 728–744. <https://doi.org/10.1111/j.1365-2699.2008.02038.x>
- Descombes, P., Walthert, L., Baltensweiler, A., Meuli, R.G., Karger, D.N., Ginzler, C. et al. (2020) Spatial modelling of ecological indicator values improves predictions of plant distributions in complex landscapes. *Ecography*, 43, 1448–1463. <https://doi.org/10.1111/ecog.05117>
- Diamond, J.M. (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, 7, 129–146. [https://doi.org/10.1016/0006-3207\(75\)90052-X](https://doi.org/10.1016/0006-3207(75)90052-X)
- Drakare, S., Lennon, J.J. & Hillebrand, H. (2006) The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecology Letters*, 9, 215–227.
- Ehlers, J. & Gibbard, P.L. (2007) The extent and chronology of Cenozoic Global Glaciation. *Quaternary International*, 164, 6–20. <https://doi.org/10.1016/j.quaint.2006.10.008>
- Epard, J.L., Gex, P. & Vust, M. (2020) Les blocs erratiques propriété de la Société Vaudoise des Sciences Naturelles. *Bulletin De La Société Vaudoise Des Sciences Naturelles*, 99, 29–66.
- Fahrig, L. (2020) Why do several small patches hold more species than few large patches? *Global Ecology and Biogeography*, 29, 615–628.
- Fattorini, S., Borges, P.A., Dapporto, L. & Strona, G. (2017) What can the parameters of the species–area relationship (SAR) tell us? Insights from Mediterranean islands. *Journal of Biogeography*, 44, 1018–1028.
- Gonggrijp, G.P. (2000) Planning and management for geoconservation. In: Baretino, D., Wimbledon, W.A.P. & Gallego, E. (Eds.) *Geological Heritage: its conservation and management*. Madrid: Instituto Tecnológico Geominero de España, pp. 29–45.
- Hallingbäck, T. & Hodgetts, N. (2000) *Status survey and conservation action plan for bryophytes: mosses, liverworts and hornworts*. Cambridge: IUCN.
- Halvorsen, R. (2012) A gradient analytic perspective on distribution modelling. *Sommerfeltia*, 35, 1–165. <https://doi.org/10.2478/v10208-011-0015-3>
- Hepenstrick, D. (2021) *Grimmia montana*. In: Bergamini, A., Boch, S., Hepenstrick, D., Kiebacher, T., Lüth, M., Moser, T., Müller, N. & Schnyder, N., (Eds.) *Beiträge zur bryofloristischen Erforschung der Schweiz - Folge 16*. Meylania 67, pp. 8–21. <https://doi.org/10.21256/zhaw-23419>
- Hill, M.O. (1979) *DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Ithaca: Cornell University.
- Hill, M.O., Preston, C.D., Bosanquet, S.D.S. & Roy, D.B. (2007) *BRYOAT T Attributes of British and Irish mosses, liverworts and hornworts*. Cambridgeshire: Centre for Ecology and Hydrology.
- Hill, M.O., & Gauch, H.G. (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio*, 42, 47–58. <https://doi.org/10.1007/BF00048870>
- Hjort, J., Gordon, J.E., Gray, M. & Hunter, M.L. (2015) Why geodiversity matters in valuing nature's stage. *Conservation Biology*, 29, 630–639. <https://doi.org/10.1111/cobi.12510>
- Imbrie, J. & Imbrie, K.P. (1986) *Ice Ages: solving the mystery*. Cambridge: Harvard University Press.
- Ingerpuu, N., Vellak, K. & Ehrlich, L. (2018) Revised red data list of Estonian bryophytes. *Folia Cryptogamica Estonica*, 55, 97–104. <https://doi.org/10.12697/fce.2018.55.10>
- Itescu, Y. (2019) Are island-like systems biologically similar to islands? A review of the evidence. *Ecography*, 42, 1298–1314. <https://doi.org/10.1111/ecog.03951>
- Jarvis, A., Reuter, H.I., Nelson, A. & Guevara, E. (2008) *Hole-filled seamless SRTM data V4*. International Centre for Tropical Agriculture. <http://srtm.csi.cgiar.org>
- Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. (2017) Climatologies at high resolution for the earth's

- land surface areas. *Scientific Data*, 4, 1–20. <https://doi.org/10.1038/sdata.2017.122>
- Kiebacher, T., Keller, C., Scheidegger, C. & Bergamini, A. (2017) Epiphytes in wooded pastures: isolation matters for lichen but not for bryophyte species richness. *PLoS One*, 12, e0182065. <https://doi.org/10.1371/journal.pone.0182065>
- Kimmerer, R.W. & Driscoll, M.J.L. (2000) Bryophyte species richness on insular boulder habitats: the effect of area, isolation, and microsite diversity. *The Bryologist*, 103, 748–756. [https://doi.org/10.1639/0007-2745\(2000\)103%5B0748:Bsroib%5D2.0.Co;2](https://doi.org/10.1639/0007-2745(2000)103%5B0748:Bsroib%5D2.0.Co;2)
- Körner, C. (2007) The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, 22, 569–574. <https://doi.org/10.1016/j.tree.2007.09.006>
- Korner-Nievergelt, F., Roth, T., Von Felten, S., Guélat, J., Almasi, B. & Korner-Nievergelt, P. (2015) *Bayesian data analysis in ecology using linear models with R, BUGS, and STAN*. Amsterdam: Elsevier.
- Krawiec, F. (1938) *Flora epilityczna glazow narzutowych zachodniej polski*. Poznan: Jachowskiego.
- Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmli, W. et al. (2010) *Flora indicativa: ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*. Bern: Haupt.
- Larson, D.W., Matthes, U. & Kelly, P.E. (2000) *Cliff ecology: pattern and process in cliff ecosystems*. Cambridge: Cambridge University Press.
- Lawyer, J. & Haas, J. (2008) *Adirondack rock, a rock climber's guide*. Pompey, NY: Adirondack Rock Press.
- Liu, H.Y., Økland, T., Halvorsen, R., Gao, J.X., Liu, Q.R., Eilertsen, O. & Bratli, H. (2008) Gradient analyses of forests ground vegetation and its relationships to environmental variables in five subtropical forest areas, S and SW China. *Sommerfeltia*, 32, 1–196. <https://doi.org/10.2478/v10208-011-0012-6>
- Lovett, G.M. & Kinsman, J.D. (1990) Atmospheric pollutant deposition to high-elevation ecosystems. *Atmospheric Environment Part A*, 24, 2767–2786. [https://doi.org/10.1016/0960-1686\(90\)90164-I](https://doi.org/10.1016/0960-1686(90)90164-I)
- MacArthur, R.H. & Wilson, E. (1967) *The theory of island biogeography*. Princeton: Princeton University Press.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. & Hornik, K. (2019) *Cluster: cluster analysis basics and extensions, v.2.1.0*. <https://CRAN.R-project.org/package=cluster>
- Mazenauer, D., Holderegger, R., Krüsi, B. & Hepenstrick, D. (2014) Populationsentwicklung und Gefährdung von *Asplenium septentrionale* auf Findlingen im Schweizer Mittelland und Jura. *Bauhinia*, 25, 37–50.
- Meier, M.K., Urmi, E., Schnyder, N., Bergamini, A. & Hofmann, H. (2013) *Checkliste der Schweizer Moose*. Zürich: Nationales Inventar der Schweizer Moosflora.
- Meylan, C. (1912) La flore bryologique des blocs erratiques du Jura. *Bulletin De La Société Vaudoise Des Sciences Naturelles*, 48, 49–70. <https://doi.org/10.5169/seals-269347>
- Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A. et al. (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science*, 19, 3–264. <https://doi.org/10.1111/avsc.12257>
- Nebel, M. & Philippi, G. (eds) (2000) *Die moose baden-württembergs*. Stuttgart: Ulmer.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2019) *Vegan: community ecology package*.
- Philippe, M. (2010) Bryophytes saxicoles calcarifuges sur substrats exotiques dans l'Ain. *Les Nouvelles Archives De La Flore Jurassienne Et Du nord-est De La France*, 8, 213–218.
- Quinn, J.F. & Harrison, S.P. (1988) Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia*, 75, 132–140. <https://doi.org/10.1007/BF00378826>
- R Core Team (2017) *R: A Language and environment for statistical computing*. Wien: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reynard, E. (2004) Protecting stones: conservation of erratic blocks in Switzerland. In: Prikryl, R. (Ed.) *Dimension stone 2004*. Balkema, Leiden: New perspectives for a traditional building material, pp. 3–7.
- Ritz, C. & Streibig, J.C. (2008) *Nonlinear regression with R*. Berlin: Springer.
- Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- Schnyder, N., Bergamini, A., Hofmann, H., Müller, N., Schubiger-Bossard, C. & Urmi, E. (2004) *Rote Liste der gefährdeten Moose der Schweiz*. Wald und Landschaft, Bern: Bundesamt für Umwelt.
- Siebel, H.N., Bijlsma, R.J. & Sparrius, L.B. (2013) *Basisrapport voor de rode lijst mossen 2012*. Utrecht: Bryologische en Lichenologische Werkgroep.
- van Son, T.C., Halvorsen, R., Norling, K., Bakke, T., Kaurin, M. & Melsom, F. (2014) Identification of fine-scale marine benthic ecoclines by multiple parallel ordination. *Journal of Marine Biology*, 462529, 1–23. <https://doi.org/10.1155/2014/462529>
- Tukiainen, H., Kiuttu, M., Kalliola, R., Alahuhta, J. & Hjort, J. (2019) Landforms contribute to plant biodiversity at alpha, beta and gamma levels. *Journal of Biogeography*, 46, 1699–1710. <https://doi.org/10.1111/jbi.13569>
- Ulrich, W., Almeida-Neto, M. & Gotelli, N.J. (2009) A consumer's guide to nestedness analysis. *Oikos*, 118, 3–17. <https://doi.org/10.1111/j.1600-0706.2008.17053.x>
- Ulvinen, T., Syrjänen, K. & Anttila, S. (eds) (2002) *The bryophytes of Finland: distribution, ecology, threats (in Finnish)*. Helsinki: Edita Publishing.
- Virtanen, R. & Oksanen, J. (2007) The effects of habitat connectivity on cryptogam richness in boulder metacommunity. *Biological Conservation*, 135, 415–422. <https://doi.org/10.1016/j.biocon.2006.10.013>
- Wächter, H.J. (1996) Zur Moosvegetation von Findlingen zwischen Ems und Weser. *Osnabrücker Naturwissenschaftliche Mitteilungen*, 22, 89–110.
- Webster, C., Mazzotti, G., Essery, R. & Jonas, T. (2020) Enhancing airborne LiDAR data for improved forest structure representation in shortwave transmission models. *Remote Sensing of Environment*, 249, e112017. <https://doi.org/10.1016/j.rse.2020.112017>
- Weibull, H. (2001) Influence of tree species on the epilithic bryophyte flora in deciduous forests of Sweden. *Journal of Bryology*, 23, 55–66. <https://doi.org/10.1179/jbr.2001.23.1.55>
- Weibull, H. & Rydin, H. (2005) Bryophyte species richness on boulders: relationship to area, habitat diversity and canopy tree species. *Biological Conservation*, 122, 71–79. <https://doi.org/10.1016/j.biocon.2004.07.001>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Detailed information on boulder selection and sampling

Appendix S2. List of data sets from which coordinates of erratic boulders were retrieved

Appendix S3. Overview table of the study areas and the number of erratic boulders

Appendix S4. Definition of the species aggregates used

Appendix S5. Non-metric multi-dimensional scaling (NMDS) of bryophyte species composition



Appendix S6. Table of correlations between the analysed variables and the NMDS axes

Appendix S7. Table of indicator species for *k*-means clusters

Appendix S8. Boxplots comparing the analysed variables between *k*-means clusters

Appendix S9. List of all bryophyte species recorded

Appendix S10. Figure 2 with the largest boulder (outlier) removed

Appendix S11. Incidence plots visualising the matrices used for analysis of nestedness

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