Forum

# What defines insularity for plants in edaphic islands?

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The theory of island biogeography postulates that size and isolation are key drivers of biodiversity on islands. This theory has been applied not only to true (e.g. oceanic) islands but also to terrestrial island-like systems (e.g. edaphic islands). Recently, a debate has opened as to whether terrestrial island-like systems function like true islands. However, identifying the effect of insularity in terrestrial systems is conceptually and methodologically challenging because recognizing species source(s) and measuring isolation is not as straightforward as for true islands. We contribute to the debate by proposing an approach to contextualize the definition of insularity and to identify the role of isolation in terrestrial island-like systems. To test this approach, we explored the relationship between insularity predictors and specialist species richness of edaphic islands in three systems in Europe (spring fens, mountaintops, and outcrops). We detected that insularity affected specialist richness of edaphic islands through island size and target effect (i.e. an emergent property of islands depending on their isolation and size). As predicted by the Theory of Island Biogeography, species richness decreased with increasing isularity. Given the comprehensiveness and ease of implementation of our approach, we encourage its extension to other island-like systems.

Keywords: terrestrial island-like system, island biogeography, island size, isolation, specialist species richness, target effect.

#### **Introduction:** The island biogeographic context

Insular systems, including true islands and other island-like environments, are excellent models to examine the biogeographic forces shaping biodiversity (Carlquist 1974, Lomolino 2000a, Patiño et al. 2017, Ottaviani et al. 2020). Traditionally, insular systems have been explored through the lens of the theory of island biogeography, in which island size and distance from the mainland (i.e. isolation) are the core drivers of diversity (MacArthur and Wilson 1967, Whitehead and Jones 1969, Lomolino 2000b) (Table 1). Recently, a debate has opened whether the biodiversity of

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Table 1. Glossary.	
Term	Definition
Connectivity	The state of being connected. Connectivity reduces isolation by joining isolated elements and allowing fluxes of energy, matter and organisms
Edaphic island	A special case of a habitat island; landscape patch characterized by distinct soil conditions that make it dissimilar from the surroundings
Habitat fragment	One of the pieces of a formerly continuous, broadly-distributed habitat type; it can be created by anthropogenic changes (e.g. land-use) or natural phenomena (e.g. water-level fluctuations)
Habitat island	Landscape patch of a distinct habitat type surrounded by other, dissimilar habitat(s)
Insularity	The state of being an island. By extension, the possibility/ability to operate as an island, i.e. to be isolated
Insularity effect	The effect of insularity-related variables (i.e. island size and isolation, taken separately or in conjunction) on biodiversity (e.g. species richness or functional diversity)
Island-like system	Any spatially defined (and confined) system resembling true island(s)
Isolation	The state of being spatially separated from a similar ecosystem by a surrounding landscape inhospitable to the establishment, e.g. water for true islands
Species source	A continent or a large island which harbors large species populations from which species may migrate and possibly colonize other islands
Target effect	The increased probability of a larger island to be colonized by random dispersal than a smaller island given a similar distance to the same species source. It is a correction of the spatial isolation of an island by its size
True island	Landmass isolated from other landmasses by water

Key terms and definitions used in this study (Dawson et al. 2016, Itescu 2019, Carter et al. 2020, Flantua et al. 2020, Ottaviani et al. 2020).

island-like systems – such as edaphic islands (Harrison 1997, Harrison et al. 2006), mountaintops (Sklenář et al. 2014, Jiménez-Alfaro et al. 2021) and inselbergs (Henneron et al. 2019) – is ruled by size and isolation in the same way as for true (e.g. oceanic) islands (Itescu 2019).

Table 1 Classes

Before assessing biodiversity patterns in terrestrial islandlike systems (Table 1), we need to acknowledge that 'insularity' is a broad concept that may apply to discontinuous and/or fragmented environments across different geographic and ecological scales (Itescu 2019). To better understand the effect (or lack of thereof) of insularity in terrestrial islandlike systems' biota, it is necessary to analyze and contextualize the meaning and role of island size and isolation case-by-case (McGann 2002, Dawson et al. 2016, Itescu et al. 2020). Our main research goal in this work is to explore whether insularity affects the species richness in edaphic island systems. We did so by 1) defining key concepts related to insularity, 2) reviewing suitable insularity metrics, and finally 3) exploring the relationship between insularity metrics and the species richness of habitat specialist plants in three edaphic island systems.

#### Defining insularity for edaphic islands

In this study, we focus on edaphic island systems generated by the discontinuous geographic distribution of specific soil types across the landscape (Kruckeberg 1991, Harrison 1997, Harrison et al. 2006) (Table 1). The scattered spatial distribution and the differences in the area among edaphic patches generate gradients of size and isolation resembling those of true islands (Fig. 1). Although biogeographic patterns in edaphic island systems have been studied for a few decades (Kruckeberg 1991, Tapper et al. 2014, Goedecke et al. 2020), the incorporation of ecological insights related to habitat specialization (Horsák et al. 2012, Horsáková et al. 2018, Ottaviani et al. 2020) and isolation components (Diver 2007, Weigelt and Kreft 2013, Carter et al. 2020) may improve our understanding of the effect of insularity on edaphic island biota. Indeed, island size and isolation are usually studied together (MacArthur and Wilson 1967, Lomolino 2000a, Whittaker et al. 2008). However, while the size is an intrinsic physical feature of any multidimensional object, isolation is the truly distinctive and defining feature of islands, largely determining its insular eco-evolutionary dynamics (Whittaker and Fernández-Palacios 2006, Losos and Ricklefs 2009, Cox et al. 2016).

For true islands, isolation is defined as the geographic distance between a given island and its species source (i.e. the nearest continent or one of the largest and species-richest islands in the same archipelago) (MacArthur and Wilson 1967, Whitehead and Jones 1969) (Table 1). Species sources are defined by two key characteristics, both linked to size: 1) species sources have more species than islands. Because of their larger area, species sources can accumulate a higher number of species. Also, larger areas often imply higher habitat diversity, which has a positive effect on species richness (Hortal et al. 2009, Keppel et al. 2016); 2) species sources are less affected by local extinctions compared to islands. This is because the larger area of species sources is associated with availability of resources, and different habitat types (MacArthur and Wilson 1967, Whittaker and Fernández-Palacios 2006, Losos and Ricklefs 2009).

For true islands, water corresponds to the matrix working as an effective barrier, equally inhospitable for all terrestrial organisms regardless of their habitat specialization. For edaphic islands, widely distributed soil types in the landscape form a matrix that would represent an inhospitable habitat only for the establishment of the species specialized to the distinct edaphic conditions forming the islands (Horsák et al. 2012, Horsáková et al. 2018, Ottaviani et al. 2020). Therefore, isolation in edaphic islands occurs in terms of the geographic distance between an edaphic patch and its species source. Given the lack of a direct equivalent of a continent,



Figure 1. Comparison between true islands (A), edaphic islands (B), and fragmented habitats (C). For more details on definitions, refer to Table 1 and Supporting information.

one or several islands in the edaphic island system are likely to play this role (Table 1; Fig. 1). Within such 'terrestrial archipelagos', we may expect that edaphic islands with the largest size and highest specialist species richness will putatively serve as species sources for the rest of edaphic islands. Although matrix-derived species also occur on edaphic islands, they are expected to be less sensitive to the differences in edaphic conditions between the island and the landscape matrix, thus experiencing less isolation than specialists (Horsák et al. 2018, Horsáková et al. 2018, Dembicz et al. 2020, Goedecke et al. 2020) (Fig. 1).

Besides specialization, dispersal is another important driver of colonization (Yeakley and Weishampel 2000, Fattorini 2009, Aranda et al. 2013, Dambros et al. 2020). Whereas specialization informs about the capacity of species to establish or not on the landscape matrix (Horsák et al. 2012, Horsáková et al. 2018, Ottaviani et al. 2020), dispersal determines whether interisland distances are large enough to prevent species movement across the archipelago (Hájek et al. 2011, Carvalho and Cardoso 2014, Horsák et al. 2015, Irl et al. 2015). Whether interisland distances are not sufficient to prevent effective colonization of edaphic island specialists, this may trigger metapopulation dynamics (Mouquet and Loreau 2003, Leibold et al. 2004). Additionally, dispersal does not only depend on the maximum dispersal distances of the target species (Tamme et al. 2014, Morgan and Venn 2017), but other factors like topography and physical barriers are also important determinants of colonization (Yeakley and Weishampel 2000, Fattorini 2009, Dambros et al. 2020). Therefore, the role of dispersal applies to both true and edaphic islands in a similar way.

On true islands, there is a positive relationship between area, resource availability, and habitat diversity (Table 1) (Hortal et al. 2009, Weigelt and Kreft 2013, Keppel et al. 2016, Henneron et al. 2019). However, on edaphic islands, resource availability and habitat diversity are often homogeneous because each edaphic island corresponds to a single patch of a distinct habitat type characterized by similar soil parameters. Regarding colonization, island size and spatial isolation may operate independently, but they may also combine to produce an emerging property known as the target effect (MacArthur and Wilson 1967, Whitehead and Jones 1969, Lomolino 1990) (Table 2; Fig. 2). Although long-recognized as an intrinsic property of true islands, the target effect has been rarely mentioned in the biogeographic literature (Stracey and Pimm 2009, Fattorini 2010, Carter et al. 2020, Hauffe et al. 2020), and it remains untested in the context of edaphic islands.

#### Insularity metrics for edaphic islands

Based on a comprehensive literature screening, we selected nine isolation metrics most commonly used and informative in island biogeography (Gilpin and Diamond 1976, Table 2. Insularity metrics used in this study.

Insularity metric	Abbreviation	Description
Island size	Size	Target edaphic island size
Nearest neighbor distance	NND	Distance from the target edaphic island to the closest edaphic island
Distance to the nearest species source	DNSS	Distance from the target edaphic island to the closest putative species source
Stepping-stone path to the species source	SSP	The shortest possible path from the target edaphic island to the closest putative species source; the path is composed of islands of the same habitat as the target edaphic island (stepping-stones)
Number of stepping stones	NSS	Number of islands of the same habitat as the target edaphic island between the target edaphic island and the putative species source
Largest gap in the stepping-stone path to the species source	LGSSP	The longest distance among all pairs of stepping stones (see SSP)
Number of islands in a buffer radius	NIB	Number of neighboring edaphic islands surrounding the target island established at two scales: local (NIB1) and landscape (NIB2). System-specific and context-dependent
Target effect	TE	Natural logarithm of the quotient between the DNSS and the square root of Size (Fig. 2)

Gilpin 1980, Calabrese and Fagan 2004, Diver 2007, Weigelt and Kreft 2013, Carter et al. 2020, Itescu et al. 2020) (Supporting information). The selected metrics capture different isolation components, namely distance to species source, stepping stones and island network (Carter et al. 2020) (Table 2). The calculation of some of these metrics relies on the identification of putative species sources, as well as on the mapping of all the edaphic islands in the study area. Details about the calculations of insularity metrics are provided in Supporting information. Because species sources for true islands are characterized by a large size and high species richness (MacArthur and Wilson 1967, Carvajal-Endara et al. 2017, Ottaviani et al. 2020) (Fig. 1), we adapted this assumption to edaphic islands by identifying as putative species sources those patches that scored above the third quartile of data distribution for both island size and species richness of specialist plants (hereafter third quartile approach).

# Testing the approach in different edaphic island systems

Here, we focused on three different edaphic island systems in Europe: 1) calcareous spring fens in the western Carpathians (Slovakia and the easternmost Czech Republic; hereafter fens); 2) acidic alpine grasslands in Cantabrian mountaintops (northwestern Spain; hereafter mountaintops) and; 3) shallow-soil acidophilous grasslands in Moravian granite outcrops (southern Czech Republic; hereafter outcrops) (Fig. 3). We worked with vascular plant specialist species of each focal



Figure 2. Schematic representation of the target effect. (A) Target effect as an emergent property of multidimensional objects (such as islands) – hitting the target is harder with increasing distance and decreasing size. (B) The target effect applies to both true and edaphic islands because with increasing distance and decreasing size, they have a lower probability of being colonized.



Figure 3. Geographical setting and characteristics of the studied edaphic island systems: western Carpathian calcareous fens (A), Cantabrian acidic mountaintops (B), Moravian granite outcrops (C). Red-filled dots correspond to putative species sources, black-filled dots to floristically surveyed habitat patches and empty dots to non-surveyed patches of the focal habitat.

habitat type (edaphic island). These species are exclusively or tightly associated with the edaphic islands, unable to establish viable populations elsewhere in the landscape matrix.

Briefly, in fens, floristic data were collected at a single 4 m  $\times$  4 m plot located at the central part of each island (Horsák et al. 2012, Horsáková et al. 2018). The species inventory at each island was completed by a floristic census of the whole edaphic island. In mountaintops, a total of 284 vegetation plots (size between 10 and 40 m<sup>2</sup>) were used to sample alpine grasslands in isolated patches on acidic bedrock, with number of plots per island associated with island area. In outcrops, sampling was performed using four 0.5 m  $\times$  0.5 m plots per island and complemented by a census of the whole edaphic island, similarly to what was done for fens. We gathered data on 49 edaphic islands for fens, 25 for mountaintops, and 20 for outcrops (Fig. 3). Expert-based selection of habitat specialists was carried out in each study system (Supporting information).

#### Biogeographic data

We identified and delimited the edaphic islands by combining different techniques. In fens, all known patches found in the western Carpathians were manually georeferenced using a GPS device (Garmin GPSMAP 62st; Horsák et al. 2012, 2018, Horsáková et al. 2018). For mountaintops, we built an edaphic island map by selecting edaphic islands above the regional treeline (1800 m a.s.l.) as those occurring on acidic bedrock only. We differentiated alpine grasslands from rocky and shrub areas based on the Normalized Difference Vegetation Index (NDVI) taken from Sentinel (USGS 2019). For outcrops, the location of edaphic islands was obtained through two sources: a field survey using a GPS device (Garmin eTrex 30×) and a vegetation map provided by the Nature Conservation Agency of the Czech Republic (Härtel et al. 2009). All the GPS points, satellite data, maps and polygon layers were processed and analyzed using QGIS desktop (QGIS 2020) and the Semi-Automatic Classification Plugin (Congedo 2016). All distance-related metrics were calculated using direct aerial Euclidean distance without considering differences in the terrain elevation.

We calculated all the insularity metrics presented in Table 2 for each edaphic island in each system (Supporting information). Using the third-quartile approach described above, we recognized seven potential species sources for fens, five for mountaintops and three for outcrops. However, when calculating the stepping-stone paths (Table 2), we found that some patches preselected as potential species sources were more likely serving as stepping stones (i.e. there were two possible species sources, one located at the nearest Euclidean distance and one located along the stepping-stone path). After correcting this issue (through testing model performance using different numbers of possible species sources), the number of putative species sources was reduced to three for fens and one for outcrops. No reduction was necessary for mountaintops. For fens only (data not available for the other systems), we also considered age of the edaphic island dated on  $C^{14}$  of the basal peat layer as an extra indicator of (temporal) isolation (Hájek et al. 2011, Horsák et al. 2015).

#### Data analysis

First, we checked the normality and linearity of our data. We evaluated the Variance Inflation Factor and tested the multicollinearity between insular predictors (Johnson and Omland 2004, Zuur et al. 2010) (Supporting information) using the function 'vif' in the R package usdm (Naimi et al. 2014). Non-collinear predictors were then used in Generalized Linear Models (GLMs) to explore the effect of insularity metrics on specialist species richness in each of the three study systems (Table 2 and Supporting information). Discarded variables, full models, error distribution and links are available in Supporting information. GLMs were fitted using the built-in R function 'glm'. After fitting GLMs containing all selected predictors for each edaphic island system, we performed an automated model selection procedure (Burnham and Anderson 2002, Wagenmakers and Farrell 2004) based on AICc ranking criteria, using the function 'dredge' in the package MuMIn (Bartoń 2019). From the full set of possible models, we selected those with a delta AICc < 4 and performed model averaging (Burnham and Anderson 2002) using the function 'model.avg' (package MuMIn). As results of the model averaging, we obtained AICc weight, standardized model coefficient, 95% confidence interval and standard error related to each predictor. All the analyses were performed in R ver. 3.6.1 (R<https://www.R-project.org>).

#### Results

In fens, island size and target effect had the strongest effect on the richness of plant specialists (Fig. 4 and Supporting information). The effect of island size was positive (i.e. larger edaphic islands hosted more specialist species), while the impact of target effect was negative (i.e. fewer specialist species were found on smaller and more isolated edaphic islands). On mountaintops, the species richness of plant specialists was positively linked to island size (Fig. 4 and Supporting information) but it was not significantly related to any other insularity metrics. On outcrops, target effect was the only important predictor (yet only marginally significant at p < 0.1) of habitat specialist species richness (Fig. 4 and Supporting information). This relationship was negative, implying that smaller and more isolated edaphic islands hosted fewer habitat specialist species than larger and less isolated ones.

#### The effect of insularity on edaphic island plants

The extension of the theory of island biogeography (MacArthur and Wilson 1967) to terrestrial island-like systems has been debated recently (Itescu 2019). Our study contributes to the debate by defining and testing what insularity may mean in edaphic islands.



Figure 4. Effects of insularity metrics on the species richness of plant specialist for the studied edaphic island systems. Circles represent predictor standardized averaged model coefficients and lines 95% confidence intervals. Solid circles and lines denote the most important (i.e. informative and significant) insular predictors of edaphic island specialist species richness. For abbreviations, refer to Table 2. Full model outputs are provided in Supporting information. Significance levels: \*\* < 0.001; \* < 0.01; \* < 0.05; < 0.1

# The role of island size and target effect in predicting species richness

Island size and target effect emerged as the best predictors of edaphic island specialist species richness (Fig. 4 and Supporting information). The positive effect of island size on species richness aligns with the extensive body of evidence in the field of island biogeography (Kalmar and Currie 2006, Kreft et al. 2008, Weigelt and Kreft 2013, Matthews et al. 2016, Whittaker et al. 2017, Ibanez et al. 2018). Indeed, larger edaphic islands confirmed their ability to host more plant specialist species in fens and mountaintops, and indirectly (through target effect) for outcrops.

However, isolation is what uniquely defines true islands; by extension, isolation should also be a key driver of species richness on edaphic islands (Patiño et al. 2017, Itescu 2019, Ottaviani et al. 2020). In our study, isolation occurred in the form of target effect – an emergent property of islands describing that they become harder targets to be colonized with increasing isolation and decreasing size (MacArthur and Wilson 1967, Gilpin and Diamond 1976, Stracey and Pimm 2009) (Fig. 2). Because target effect incorporates island size and isolation into one metric, it may capture the effect of insularity on biota more comprehensively than island size and isolation separately (MacArthur and Wilson 1963, Whitehead and Jones 1969, Gilpin and Diamond 1976). Additionally, target effect is dimensionless and easy to measure, especially when compared to more elaborated and timeconsuming connectivity metrics (Tischendorf and Fahrig 2000, Diver 2007, Weigelt and Kreft 2013, Carter et al. 2020). Such properties make this metric very suitable for biogeographic studies.

#### Biogeographic insights into the studied edaphic island systems

We identified that the plant species occurring in the three edaphic island systems experience different degrees of insularity generated by differences in the effect of island size and isolation. For the western Carpathian fens (timesince-formation being approximately 17 Ky; Hájek et al. 2011, Horsák et al. 2015), we revealed the strongest effect of insularity on edaphic island plant specialists, with both island size and target effect playing a key role in shaping the richness of specialists. Additionally, the largest fens also tended to be the oldest and least spatially isolated, further supporting the highest richness of habitat specialists (Horsák et al. 2012). Age provides an estimate of temporal isolation (Nekola 1999, Flantua et al. 2020). However, age and distance to the species source as single predictors did not significantly explain specialist richness in fens.

For Cantabrian mountaintops, edaphic island specialist richness was driven solely by island size. Although a tight species-area relationship is an important property of any insular system (Aranda et al. 2013, Whittaker et al. 2017, Henneron et al. 2019), isolation metrics and target effect did not affect plant specialists. Therefore, the insularity of this system remains doubtful. One possible explanation for the lack of isolation effect in this island-like system may be related to the temporal dynamics of alpine grasslands, which have been historically connected in glacial periods, favoring the immigration of species to new areas through temporary bridges (Flantua et al. 2020), and the persistence of small populations in restricted areas during interglacial periods such as the present (Jiménez-Alfaro et al. 2016).

For Moravian outcrops, target effect was the most important predictor of edaphic island specialist richness, yet its effect was less pronounced than for fens (Fig. 4 and Supporting information). This finding may indicate that, although this system is distinguished by a certain degree of insularity, there are other important ecological drivers that are independent of biogeographic predictors, such as long-term management regimes including grazing pressure, mowing frequency and abandonment (Buchholz et al. 2018).

Finally, no effects of connectivity metrics (i.e. stepping stones and island network) on specialist richness as found in all the three case studies may indicate that our edaphic island systems resemble more true islands than fragmented habitats ruled by metapopulation dynamics (Fahrig 2003) (Fig. 1). In that context, landscape connectivity among the patches is expected to be an important driver of species richness and composition (Mouquet and Loreau 2003, Leibold et al. 2004, Saura et al. 2014, Hanski 2015, Flantua et al. 2020).

#### **Conclusions and future directions**

This study provides a conceptual framework and methodological tools to address a hot topic for island biogeography: whether terrestrial island-like systems (edaphic islands in this case) function as true islands (Patiño et al. 2017, Itescu 2019, Ottaviani et al. 2020). We were able to identify an effect of insularity on the richness of edaphic island plant specialists across different systems. Our findings suggest that the proposed approach is applicable in areas with different environmental conditions (e.g. climate, geology, soil) and spatial scales (fens and mountaintops are distributed over areas spanning tens to hundreds of kilometers, whereas outcrops only across a few kilometers).

We acknowledge that including the role of dispersal would have been ideal because may provide insights into the mechanisms driving colonization on edaphic islands. This approach, however, would require information about the maximum dispersal distance for either all or the vast majority of specialist species so to identify good or bad dispersers. Then, good dispersers should be removed from the models so focusing only on those specialists with limited dispersal abilities (hence, accounting for metapopulation dynamics). Unfortunately, plant traits related to dispersal were not available in a sufficient amount that would have allowed us to reliably identify good and bad dispersers for the three edaphic island systems. Finally, in the absence of data on dispersal, our approach based on the identification of edaphic island specialists appears more conservative.

We encourage broader scrutiny and implementation of the proposed approach to other terrestrial island-like systems, including those dominated by different growth forms than herbs (e.g. woody plants in isolated forest patches; Coelho et al. 2018) or where the difference between islands and the landscape matrix is not defined by edaphic conditions (e.g. elevation; Sklenář et al. 2014). In other systems, we cannot rule out that different island biogeography predictors (alone or in combination) may effectively capture the effect of insularity on island biota. *Acknowledgements* – We thank the journal editors and three anonymous reviewers for providing insightful comments during the review process.

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#### **Authors contributions**

FEMC conceived the research idea and ran the analyses; FEMC and GO wrote the first draft of the manuscript and led the writing; MCh, MHá, MHo, BJ-A and DZ collected and prepared the floristic data; all co-authors contributed to the analytical setup and revisions of the manuscript.

#### **Transparent Peer Review**

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#### Data availability statement

All data is provided in the Supporting information.

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Further comparison between oceanic islands, edaphic islands, and fragmented habitats.								
	True (ocanic) islands	Edaphic islands	Fragmented habitats					
Species source	Fixed and well-defined, usually a continent.	Fixed but putative, generally one of the largest edaphic island(s).	Dynamic and undefined, patches may act as both sinks or sources.					
Habitat types	Several habitats may occur on a single island.	All patches belong to a single habitat type.	All fragments correspond to a single habitat type.					
Specialists vs generalists	Each individual landmass is an island for both specialists and generalists.	Each patch is an island mainly for habitat specialists.	Habitat fragments serve as islands neither for specialist nor generalists.					
Matrix dissimilarity	The ocean constitutes an inhospitable matrix preventing the establishment of all the species from the terrestrial habitats.	The matrix is dissimilar, inhospitable and, to some degree, impermeable mainly for edaphic island specialists.	Habitat fragments may expand, contract, merge, disappear or re- appear in the matrix.					
Colonization	Main colonization flux is from the species source to islands. Back colonization (i.e. from islands to species source) occurs rarely.	Main colonization flux is from the species source to islands. Back colonization is likely to occur. Inter-island colonization may be important in highly connected parts of the system.	Main colonization flux is from one fragment to another fragment. Inter-fragment colonization is highly dynamic. Fragments may play different roles (sink or source) for different species and changing with time.					

### Further Description of insularity metrics

Island size corresponds to the area of the target edaphic island.

**Distance to the nearest species source** and **Nearest neighbor distance** corresponds to the Euclidean distance between a target island and its nearest putative species source or neighbor, respectively (MacArthur and Wilson 1963, 1967).

For **Number of islands in a buffer radius**, the optimal size of the buffer for measuring the amount of focal habitat depends on the spatial scale of the study system (Weigelt and Kreft 2013). Therefore, we designed independent sets of buffer radius, two for each edaphic island system (local and landscape scale), considering the distribution of their inter-island distances. We used these buffers to calculate a proxy of the available habitat to specialist species by counting the number of target edaphic islands surrounding a given target edaphic island.

Regarding connectivity metrics (**Stepping-stone path, Number of stepping stones and Largest gap in the stepping-stone path**), we built stepping-stone paths connecting the target edaphic islands with their nearest putative species source (Gilpin 1980, Carter et al. 2020). We followed two main criteria to build these paths: 1) keeping the number of stepping-stones as low as possible and 2) making sure that inter-island distances along the path never exceeded the direct distance between the target edaphic island and its putative species source. The **Largest gap in the stepping-stone path** represents the longest distance a species has to overcome to disperse from the putative source (Kalmar and Currie 2006, Diver 2007).

**Target effect** was calculated as the natural logarithm of the ratio between the Distance to the nearest species source and the square root of the Island size (Fig. 3). The conceptual origin of Target effect can be traced back to MacArthur and Wilson (1963) and Gilpin and Diamond (1976) where it was associated with immigration rates. This metric, in the way we have formulated it, rescales the distance to the species source accordingly to the size of the target island (e.g. smaller and more isolated islands should be harder to colonize, accounting fewer species, than less isolated and larger ones).

Suppleme	Supplementary Table 1 - Habitat specialist richness and biogegraphic predictors (Western Carpathian fens)											
Island ID	Plant specialist richness	Age (years)	Island size (m2)	Nearest neighbor distance (m)	Number of islands in Buffer 1 (2.8 km)	Number of islands in Buffer 2 (42 km)	Distance to the nearest species source (m)					
B10	33	10932	30000	1339	3	42	90314					
C24	14	636	912	1402	4	60	25519					
D31	26	1064	6000	1872	3	66	33002					
D32	15	4967	860	8053	1	51	45582					
G35	14	2789	820	10542	1	24	43787					
G36	14	7692	15000	1021	4	45	21577					
G39	9	469	1000	2552	2	44	103192					
H43	12	670	3380	10027	1	51	53861					
H54	21	12473	3000	2379	4	45	19254					
H57	13	730	1500	1333	2	42	111441					
H60	13	665	1520	312	5	49	93018					
J63	10	1737	700	2917	2	51	86081					
K65	14	1958	1700	578	2	44	105771					
K66	7	735	800	5707	1	46	94998					
K69	15	908	800	2342	3	45	36204					
К70	14	1738	850	218	2	42	54911					
K71	8	988	214	1308	4	57	82590					
K72	27	7449	16000	2917	2	61	32874					
K73	17	1480	1000	29	2	56	37572					
177	24	11049	18000	163	-	57	34657					
M84	11	880	530	6370	1	35	123574					
M87	26	12824	20000	3321	2	47	46259					
M89	9	426	80	5115	-	46	65716					
M90	12	813	3000	13350	1	2	98130					
M92	8	8878	2200	4303	1	54	89308					
M93	7	908	2200	2517	2	54	87175					
M94	29	12160	5000	496	2	65	496					
Ngg	10	12100	750	1333	2	42	111767					
0101	10	1681	539	2816	2	57	72/03					
P107	22	11030	15000	2010	2	60	32074					
P113	16	1621	500	275	2	61	45239					
P118	20	12020	4900	6637	1	37	6637					
P110	16	1816	1300	3/32	2	45	27965					
P140	25	10422	15000	2494	2	43	25705					
R140	23	16975	11000	496	2	44	496					
R142	28	10373	700	430	5	2	450					
S156	34	2711	2200	2946	1	52	21722					
\$150	12	6610	2350	2040	2	32	56480					
5153	12	2202	300	8330 E79	1	45	106217					
5162	12	2295	500	576	2	44	100317					
5104	10	2705	3500	449	2	54	42784					
T100	18	270	2500	4556	1	31	40176					
T170	21	1905	1130	3321	2	49	42944					
11/2	11	4399	240	1645	1	46	9001					
V1//	16	35/5	15000	3243	3	62	2/196					
V1/9	10	14075	8600	21684	1	21	28881					
V180	13	3201	1000	8407	1	5/	54098					
V191	19	8168	500	3432	3	43	25081					
V192	27	5892	10000	1339	3	45	1339					
Z202	9	641	675	6797	1	23	131620					

Suppleme	supplementary Table 2 - Habitat specialist richness and biogegraphic predictors (Cantabrian mountaintops)											
Island ID	Plant specialist richness	Age (years)	Island size (m2)	Nearest neighbor distance (m)	Number of islands in Buffer 1 (11 km)	Number of islands in Buffer 2 (48 km)	Distance to the nearest species source (m)					
58	13	-	30040434	114	10	73	8278					
73	2	-	937416	135	14	65	25139					
79	4	-	31898864	97	4	66	1941					
92	8	-	3091364	156	15	62	28367					
97	5	-	7449065	1084	3	69	9227					
100	5	-	3048664	57	20	74	4212					
104	2	-	231431	170	11	74	21076					
109	6	-	15445145	42	12	65	5361					
115	4	-	5554750	1116	7	49	8115					
118	5	-	557615	1298	13	69	12336					
126	9	-	3350411	360	13	74	15644					
140	2	-	4495245	814	5	63	7791					
144	5	-	14793219	147	12	83	7537					
149	7	-	2756251	763	4	54	11081					
154	16	-	28161550	266	11	52	32990					
162	6	-	16073301	168	12	75	1267					
167	3	-	431864	190	11	84	18881					
182	11	-	45418539	293	4	65	1881					
184	4	-	11388667	154	15	80	17056					
203	11	-	36222225	408	8	75	1881					
243	33	-	134580200	134	12	74	45100					
261	3	-	715015	553	15	65	6106					
266	4	-	216176	553	15	64	8683					
270	3	-	188952	104	11	62	9910					
271	5	-	1578438	224	14	71	9166					

#### Supplementary Table 3 - Habitat specialist richness and biogegraphic predictors (Moravian outcrops)

	•			• •			
Island ID	Plant specialist richness	Age (years)	Island size (m2)	Nearest neighbor distance (m)	Number of islands in Buffer 1 (0.2 km)	Number of islands in Buffer 2 (1 km)	Distance to the nearest species source (m)
B17	11	-	543	5	2	6	12045
B7	17	-	7719	24	1	5	10153
B8	15	-	1084	43	1	4	10458
H29	18	-	1720	306	0	2	4032
H33	10	-	931	270	0	6	6024
N1	17	-	938	108	2	7	8526
N11	15	-	777	249	0	5	6989
N12	11	-	617	249	0	4	6643
N2	18	-	3237	17	1	8	9312
N4	13	-	503	6	2	7	8618
P20	18	-	8972	346	0	4	709
P21	21	-	1512	74	1	6	347
P22	23	-	4145	179	0	6	0
P23	16	-	361	179	0	7	273
P24	18	-	5618	219	0	5	582
P26	21	-	2471	437	0	1	2213
P28	18	-	1736	437	0	2	1588
P39	14	-	824	74	1	6	376
T49	13	-	410	6	1	3	2003
V34	17	-	14115	735	0	0	9112

Length of the stepping stone path to the nearest species source (m)	Number of stepping stones	Largest gap in the stepping stone path (m)	Target effect (log[distance to the nearest species sources / sqrt (target island area)])
143663	24	19770	6.3
28862	4	13465	6.7
50398	9	8282	6.1
86371	11	23143	7.3
62511	3	23648	7.3
21633	1	19254	5.2
240429	32	23143	8.1
96398	12	23143	6.8
19254	0	19254	5.9
252353	35	23143	8.0
230689	31	23143	7.8
162085	22	23143	8.1
246282	33	23143	7.8
180231	27	23143	8.1
43598	7	19254	7.2
137736	20	23143	7.5
195021	28	23143	8.6
53311	8	19254	5.6
56292	6	15206	7.1
61831	9	19254	5.6
268338	38	23143	8.6
56628	11	19254	5.8
133879	18	23143	89
100169	2	69884	7 5
223394	29	23143	76
133836	17	23143	7.6
496	0	496	19
253685	36	23143	83
115619	14	23143	8.0
50395	7	19254	5.6
91482	16	10388	76
6637	0	6637	4.6
33086	5	19254	67
56818	8	23143	5.7
496	0	496	16
112510	3	69884	2.0
26023	2	19254	61
123475	17	23143	7 5
246860	34	23143	87
103015	15	23143	7.6
43496	5	15206	67
53307	10	19254	7 2
231887	30	23143	87
70994	11	10388	5.7
30285	1	10300	5.4
107212	12	23040	5.7 7.6
29654	15	19254	7.0
1330	4	1339	7.0
282500	40	231/2	2.0
202377	-+0	20140	0.0

Length of the stepping stone path to the nearest species source (m)	Number of stepping stones	Largest gap in the stepping stone path (m)	Target effect (log[distance to the nearest species sources / sqrt (target island area)])
16910	13	3427	0.4
19869	16	3427	3.3
1941	0	1941	-1.1
18980	15	3427	2.8
20043	16	3427	1.2
9061	6	3427	0.9
4331	2	1695	3.8
2658	1	1695	0.3
1889	2	1115	1.2
4721	2	2460	2.8
3542	2	1695	2.1
22791	17	3427	1.3
3902	2	1959	0.7
24366	19	3427	1.9
30761	23	4506	1.8
1267	0	1267	-1.2
18635	14	3606	3.4
2034	0	2034	-1.3
4075	4	1695	1.6
2034	0	2034	-1.2
18158	11	3606	1.4
6117	1	3196	2.0
6669	2	3196	2.9
7299	2	3196	3.1
9747	6	3196	2.0

Length of the stepping stone path to the nearest species source (m)	Number of stepping stones	Largest gap in the stepping stone path (m)	Target effect (log[distance to the nearest species sources / sqrt (target island area)])
9807	19	1093	6.2
8898	20	1093	4.7
8483	19	1093	5.8
4917	7	1135	4.6
6381	11	1135	5.3
8228	19	1093	5.6
5552	11	1093	5.5
5302	10	1093	5.6
7444	15	1093	5.1
8120	18	1093	6.0
647	2	346	2.0
227	0	227	2.2
0	0	0	0.0
179	0	179	2.7
553	1	326	2.0
1623	3	534	3.8
1186	2	534	3.6
301	1	227	2.6
1494	3	847	4.6
10168	21	1135	4.3

Supplementary Table 4 - Habitat specialists for Western Carpathian calcareous fens									
Island-ID	Blysmus compressus	Carex appropinquata	Carex chordorrhiza	Carex davalliana	Carex diandra	Carex dioica	Carex echinata	Carex flava	
B10	1	1	0	1	1	1	0	1	
C24	1	0	0	0	0	0	1	1	
D31	1	0	0	1	1	1	0	1	
D32	1	0	0	1	0	0	0	0	
G35	0	0	0	1	0	0	0	0	
G36	0	0	0	0	0	0	0	0	
G39	0	0	0	1	0	0	0	1	
H43	0	0	0	1	0	0	0	0	
H54	1	0	0	1	1	0	0	0	
H57	1	0	0	0	0	0	0	1	
H60	1	0	0	0	0	0	0	1	
J63	0	0	0	0	0	0	1	0	
K65	1	0	0	1	0	0	0	1	
к66	0	0	0	0	0	0	0	0	
к69	0	0	0	1	0	0	0	0	
к70	0	0	0	0	0	0	1	0	
K71	0	0	0	0	0	0	0	0	
K72	1	1	0	1	1	1	0	1	
K73	0	0	0	1	0	1	0	1	
L77	0	0	0	1	0	1	1	1	
M84	0	0	0	0	0	0	0	1	
M87	1	0	0	1	0	1	1	1	
M89	0	0	0	0	0	0	1	1	
M90	1	0	0	0	1	0	0	1	
M92	0	0	0	0	0	0	U	0	
N193	0	0	0	0	0	0	0	1	
N94	1	0	0	1	0	0	0	1	
0101	0	0	0	1	0	0	0	1	
B107	1	0	0	1	1	1	1	0	
P107	1	0	0	1	1	0	0	1	
P118	0	0	0	1	0	1	1	1	
P119	0	0	0	1	0	1	0	-	
R140	0	1	0	-	0	-	0	0	
R142	1	1	0	1	0	1	1	0	
R143	0	0	0	0	0	0	0	1	
<b>S156</b>	1	0	0	1	0	1	0	1	
S158	1	0	0	1	0	0	0	0	
<b>S162</b>	0	0	0	1	0	0	0	1	
S164	0	0	0	1	0	0	0	1	
T168	1	0	0	1	0	1	0	1	
T170	1	0	0	1	0	1	1	1	
T172	1	0	0	0	0	0	0	1	
V177	0	0	0	1	0	0	0	0	
V179	0	0	0	1	0	1	0	1	
V180	0	0	0	1	0	0	0	1	
V191	1	0	0	1	0	0	0	1	
V192	1	1	0	1	0	1	0	1	
Z202	0	0	0	0	0	0	0	1	

Supplement	Supplementary Table 5 - Habitat specialists for Cantabrian mountaintops' acidophilus grasslands										
Island-ID	Agrostis tileni	Alchemilla fulgida	Alchemilla saxatilis	Alchemilla transiens	Androsace cantabrica	Antennaria dioica	Anthemis cretica subsp. carpatica	Arabis alpina			
58	1	0	0	0	0	0	0	0			
73	0	0	0	0	0	0	0	0			
79	0	0	0	0	0	0	0	0			
92	0	0	0	0	0	0	0	0			
97	0	0	0	0	0	0	0	0			
100	0	0	0	0	0	0	0	0			
104	0	0	0	0	0	0	0	0			
109	0	0	0	0	0	0	0	0			
115	0	0	0	0	0	0	0	0			
118	1	0	0	0	0	0	0	0			
126	1	0	0	0	0	0	0	0			
140	0	0	0	0	0	0	0	0			
144	0	0	0	0	0	0	0	0			
149	0	0	0	0	0	0	0	0			
154	0	0	0	0	0	1	0	0			
162	0	0	0	0	0	0	0	0			
167	1	0	0	0	0	0	0	0			
182	0	0	1	0	0	1	0	0			
184	1	0	0	0	0	0	0	0			
203	1	0	0	0	0	0	0	0			
243	0	1	0	1	1	1	1	1			
261	0	0	0	0	0	0	0	0			
266	0	0	0	0	0	1	0	0			
270	0	0	0	0	0	0	0	0			
271	0	0	0	0	0	1	0	0			

Supplementary Table 6 - Habitat specialists for Moravian outcrops' shallow-soil acidophilus grasslands										
Island-ID	Agrostis vinealis	Artemisia campestris	Centaurea stoebe s.lat.	Dianthus deltoides	Euphrasia stricta	Festuca ovina	Festuca rupicola	Helianthemum grandiflorum s.lat.		
B17	0	0	1	0	0	1	0	0		
B7	1	0	1	0	1	1	1	0		
B8	1	0	1	1	0	1	0	0		
H29	0	0	1	0	0	1	1	1		
Н33	0	1	1	0	0	1	0	0		
N1	1	0	1	0	0	1	1	1		
N11	0	0	1	0	0	1	0	1		
N12	0	0	1	0	0	1	0	0		
N2	1	0	1	1	0	1	1	1		
N4	1	0	1	0	0	1	0	0		
P20	0	1	1	1	0	1	0	1		
P21	0	1	1	0	0	1	1	1		
P22	0	1	1	0	0	1	1	1		
P23	1	1	1	0	0	1	1	1		
P24	0	1	1	0	0	0	0	1		
P26	1	1	1	1	1	1	1	1		
P28	0	1	1	0	0	1	1	1		
P39	0	1	1	1	0	1	0	0		
Т49	0	0	1	0	0	1	0	0		
V34	0	1	1	0	0	1	1	1		

Carex hostiana	Carex lasiocarpa	Carex lepidocarpa	Carex limosa	Carex nigra	Carex panicea	Carex pulicaris	Carex viridula	Centaurium littorale ssp. uliginosu
1	0	1	1	1	1	0	0	0
0	0	0	0	1	1	0	0	0
1	0	1	0	1	1	0	0	0
1	0	0	0	0	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	0	0	1	1	0	0	1
0	0	0	0	0	1	0	0	0
0	0	1	0	1	1	0	0	0
0	0	1	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	0	0	0	1	0	0	0
0	0	1	0	1	1	0	1	0
0	0	0	0	0	1	0	0	0
1	0	1	0	1	1	0	0	0
0	0	1	0	0	1	0	0	0
0	0	1	0	1	1	0	0	0
0	0	0	0	0	1	0	0	0
1	0	1	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	0	0	0	1	0	0	0
0	0	0	0	0	1	0	0	0
1	0	1	0	1	1	0	1	1
0	0	0	0	1	1	0	0	0
0	0	1	0	0	1	0	0	0
1	0	0	0	1	1	0	0	0
1	0	0	0	0	1	0	0	0
0	0	1	0	1	1	0	0	0
1	0	1	0	1	1	0	0	0
1	0	1	0	1	1	0	1	0
1	0	1	0	1	0	0	0	0
0	0	0	0	1	1	0	0	0
1	0	1	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	1	0	0	1	0	0	0
0	0	1	0	0	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	1	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	1	0	1	1	0	0	0
0	0	0	0	1	1	0	0	0
1	0	1	0	0	1	0	0	0
1	0	1	0	1	1	0	0	0
1	0	1	0	1	1	0	0	0
0	0	0	0	0	1	0	0	0

Armeria duriaei	Bellardiochloa variegata	Botrychium lunaria	Campanula scheuchzeri	Dianthus langeanus	Festuca eskia	Festuca indigesta	Festuca summilusitana	Gentiana lutea
0	0	0	0	1	1	1	0	0
0	0	0	0	0	0	1	0	0
0	0	0	0	1	0	0	1	1
1	0	0	0	1	1	1	0	1
0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	1	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0
0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0
0	0	0	0	1	1	0	0	0
0	0	0	0	1	1	1	0	0
0	0	0	1	0	1	0	0	0
0	0	0	0	0	1	0	0	0
1	0	0	0	1	0	1	0	0
0	0	0	0	0	1	0	0	0
1	0	0	0	1	0	1	1	0
0	1	1	1	1	1	1	0	1
0	0	0	0	1	0	1	0	0
0	0	0	0	1	0	1	0	0
0	0	0	0	1	0	1	0	0
0	0	0	0	1	0	1	0	0

Helichrysum arenarium	Hieracium pilosella	Jasione montana	Jovibarba globifera	Koeleria macrantha	Lychnis viscaria	Phleum phleoides	Pimpinella saxifraga s.str.	Potentilla heptaphylla
1	0	0	0	1	1	0	1	0
1	1	1	0	1	1	0	1	0
0	1	1	0	0	0	0	1	0
1	1	0	0	1	1	1	1	0
1	0	0	0	1	0	0	1	0
0	1	1	0	1	1	0	1	0
0	1	0	0	1	1	0	1	0
1	1	1	0	0	1	0	1	0
0	1	1	0	1	1	0	1	0
1	1	1	0	0	1	0	1	0
0	1	0	0	1	1	1	1	0
0	1	1	0	1	1	1	1	0
1	1	1	0	1	1	1	1	0
0	1	0	0	1	1	0	1	0
1	1	1	0	1	1	1	1	0
0	1	0	0	1	1	1	1	0
0	1	0	1	1	1	1	1	1
0	0	0	0	1	1	1	1	0
0	1	1	0	1	1	0	1	0
1	1	0	0	1	1	1	1	0

Cladium mariscus	Dactylorhiza incarnata	Dactylorhiza maculata	Dactylorhiza majalis agg.	Drosera anglica	Drosera rotundifolia	Eleocharis quinqueflora	Epipactis palustris	Equisetum variegatum
0	1	0	1	0	1	1	1	1
0	0	0	1	0	0	1	1	1
0	1	0	1	0	0	1	1	1
0	0	0	1	1	0	1	0	0
0	1	0	1	0	0	1	1	0
0	1	0	0	0	0	1	0	0
0	0	0	1	0	0	1	0	0
0	0	0	1	0	0	1	1	0
0	1	0	1	0	0	1	1	1
0	1	0	1	0	0	0	1	0
0	1	0	1	0	0	0	1	0
0	0	0	1	0	0	1	1	0
0	0	0	1	0	0	0	1	0
0	0	0	1	0	0	0	1	0
0	0	0	1	0	0	1	0	1
0	0	0	1	0	0	1	1	0
0	1	0	0	0	0	0	1	0
0	1	0	1	0	0	1	1	1
0	0	0	1	0	0	1	1	0
U	U	0	1	0	0	1	1	0
U	U	0	1	0	0	0	1	0
0	0	0	1	0	0	1	1	0
U	U	0	1	0	0	0	1	0
U	U	0	1	0	0	0	1	0
U	U	0	1	0	0	0	1	0
0	0	0	0	0	0	0	1	0
1	1	0	1	0	0	1	1	1
0	1	0	1	0	0	0	1	0
0	1	0	0	0	0	1	1	0
0	1	0	1	0	0	1	1	0
0	0	0	1	0	0	1	0	1
0	0	0	1	0	0	1	1	0
0	0	0	1	0	0	1	0	0
0	0	0	1	1	0	1	1	0
0	0	0	1	0	1	1	1	1
0	1	0	1	0	0	1	1	0
8	1	0	1	0	0	1	1	0
0	0	0	1	0	0	1	1	0
0	0	0	0	0	0	1	1	1
Û	ů O	0	1	0	0	1	1	1
0	0	1	1	0	0	1	1	0
ő	0	0	1	0	0	0	1	0
0	0	0 0	1	0	0	1	1	1
0	0	0 0	1	0	0	1	1	0
ő	0	0	1	0	0	0	1	0
0	0	0 0	1	0	0	1	0	0
õ	1	õ	1	0	Ő	1	1	1
0	-	0	1	0	0	0	1	- 0
				-		-		

Hypericum richeri subsp. burseri	Jasione crispa	Juncus trifidus	Luzula hispanica	Luzula nutans	Lychnis alpina	Minuartia recurva	Omalotheca supina	Omalotheca sylvatica
0	1	1	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
1	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
1	0	0	0	1	0	0	0	0
1	0	0	0	1	0	0	0	0
1	1	1	1	1	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	1	0	0
1	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	1	0	0

Potentilla tabernaemontani	Pulsatilla grandis	Scleranthus perennis	Sedum acre	Sedum sexangulare	Seseli osseum	Silene nutans s.lat.	Thymus pulegioides	Verbascum chaixii ssp. austriacum
1	0	1	1	0	0	0	1	0
1	0	1	0	1	1	1	1	0
1	0	1	1	0	1	1	1	1
1	0	0	1	1	1	1	1	1
0	0	0	0	0	0	1	1	0
1	0	1	1	0	1	1	1	1
1	0	1	1	0	1	1	0	0
1	0	0	1	0	0	1	1	0
1	0	1	1	0	1	1	1	0
1	0	0	1	0	1	1	1	0
1	0	1	1	1	1	1	1	0
1	0	1	1	1	1	1	1	1
1	0	1	1	1	1	1	1	1
1	0	0	0	1	1	0	1	1
0	0	1	1	0	1	1	1	1
1	1	1	0	1	1	0	1	1
0	0	0	1	0	0	1	1	0
0	0	1	1	0	1	1	1	0
1	0	1	1	1	1	1	0	0
0	0	0	1	1	1	0	1	1

Eriophorum angustifolium	Eriophorum latifolium	Glaux maritima	Gymnadenia densiflora	Hydrocotyle vulgaris	Juncus alpinus	Juncus alpinoarticulatus	Juncus subnodulosus	Ligularia sibirica
1	1	0	1	0	0	1	0	0
1	1	0	0	0	0	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	1	0	0	0	0	0
0	1	0	0	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	1	0	1	0	0	1	0	0
1	1	0	1	0	1	0	0	0
1	1	0	0	0	1	0	0	1
1	1	0	1	0	0	0	0	0
1	1	0	0	0	1	0	0	0
1	1	0	0	0	0	0	0	0
- 1	-	0	0	0	0	0	0	0
-	- 1	0	0	0	0	0	0	0
-	- 1	0	0	0	0	0	1	0
- 1	-	0	1	0	0	0	0	0
0	-	0	-	0	0	0	0	0
1	1	0	1	0	0	0	0	0
- 1	-	0	-	0	0	0	0	0
1	1	0	1	0	0	1	0	0
1	1	0	1	0	1	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	1	0	0	1	0	0
1	1	0	1	0	0	0	0	0
- 1	- 1	0	0	0	0	0	0	0
1	1	0	0	0	1	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	1	0	1	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	1	0	0	0	0	0	0	0
1	- 1	0	0	0	0	0	0	0
1	- 1	0	1	0	0	0	0	0
- 1	- 1	0	- 0	0	0	0	0	0
1	1	0	0	0	0	1	õ	0
1	- 1	0	1	0	0	0	0	0
1	1	0	1	0	0	0	0	0
		-		-				

Oreochloa blanka	Paronychia polygonifolia	Phyteuma hemisphaericum	Plantago alpina	Potentilla crantzii	Pulsatilla vernalis	Ranunculus amplexicaulis	Rumex suffruticosus	Scorzoneroides pyrenaica
0	0	1	1	0	0	0	0	1
0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0
0	0	0	1	0	0	0	0	0
0	0	0	1	0	0	0	1	1
0	0	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	1	1	0	0	0	0	0
0	0	0	0	0	0	0	0	1
0	0	1	0	0	0	1	0	1
0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	1	0
0	1	0	1	0	0	0	0	1
0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0
0	0	1	1	0	0	0	0	1
1	1	0	1	1	1	0	0	1
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

Veronica dillenii	Veronica prostrata	Veronica verna
1	0	0
0	0	0
0	1	0
0	1	0
1	1	0
0	0	0
1	1	1
0	0	0
0	1	0
0	0	0
0	1	0
1	1	0
1	1	1
0	1	0
1	1	0
0	1	0
1	1	1
0	1	0
0	0	0
0	1	0

Liparis loeselii	Menyanthes trifoliata	Parnassia palustris	Pedicularis palustris	Pedicularis sceptrum-carolinum	Pinguicula alpina	Pinguicula vulgaris	Plantago maritima	Polygala amarella
0	1	1	1	1	0	1	0	0
0	0	1	0	0	0	0	0	0
0	1	1	1	0	0	1	0	0
0	0	1	0	0	0	0	0	1
0	0	1	0	0	0	1	0	0
0	0	1	1	0	0	1	1	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0	1
0	1	1	0	0	0	1	0	0
0	0	0	0	0	0	0	0	1
0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1
1	0	0	0	0	0	0	0	1
0	0	1	0	0	0	0	0	0
0	0	1	1	0	0	1	0	0
0	0	0	0	0	0	1	0	0
0	0	1	0	0	0	0	0	0
0	0	1	1	1	0	1	0	0
0	0	1	0	0	0	1	0	0
0	1	1	1	0	0	1	0	1
0	0	1	0	0	0	0	0	1
0	1	1	1	0	0	1	0	1
0	0	1	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	1	1	0	0	1	0	0
0	0	0	0	0	0	0	0	1
0	0	1	0	0	0	0	0	0
0	1	1	1	0	0	1	0	0
0	0	1	0	0	0	1	0	0
0	0	1	0	0	0	1	0	0
0	0	1	0	0	0	1	0	0
0	1	1	0	0	0	1	0	0
0	1	1	0	0	0	1	0	1
0	0	0	0	0	0	0	0	0
0	1	1	1	0	0	1	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	1	0	1
0	0	1	1	0	0	1	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	1	0	0
0	1	1	0	0	0	1	0	0
0	0	1	0	0	0	0	0	1
0	1	1	0	0	0	1	0	0
0	1	1	1	1	0	1	0	0
0	0	0	0	0	0	0	0	0

Sedum candolleanum	Silene acaulis	Silene ciliata	Silene foetida	Teesdaliopsis conferta	Thymelaea coridifolia subsp. dendrobryum	Trifolium alpinum
0	0	1	0	1	1	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	1	1	0
0	0	0	0	1	0	0
0	0	1	0	1	0	0
0	0	0	0	1	1	0
0	0	0	0	1	1	0
0	0	0	0	1	1	0
0	0	0	0	1	0	0
0	0	0	0	1	1	0
0	0	0	0	1	0	0
0	0	0	0	1	0	0
0	0	0	0	1	1	0
0	0	1	1	1	1	0
0	0	1	0	1	0	0
0	0	0	0	1	0	0
1	0	1	0	0	0	0
0	0	0	0	1	0	0
1	0	0	0	1	0	0
1	1	1	0	1	0	1
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0

Primula farinosa	Scheuchzeria palustris	Schoenus ferrugineus	Sesleria uliginosa	Swertia perennis	Tofieldia calyculata	Trichophorum pumilum	Triglochin maritimum	Triglochin palustre	Utricularia minor	Valeriana dioica
1	0	0	0	1	1	0	1	1	0	0
0	0	0	0	0	0	0	0	1	0	0
1	0	0	0	0	0	0	1	1	1	0
0	0	0	0	0	1	0	0	1	0	0
0	0	0	0	0	0	0	0	1	0	0
1	0	0	0	0	0	1	1	1	0	0
0	0	0	0	0	0	0	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	1	1	0	0
0	0	0	0	0	0	0	0	1	0	1
0	0	0	0	0	0	0	0	1	0	1
0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	1	0	0	1	0	0
0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	1	0	0
1	0	0	0	0	0	0	0	1	1	0
0	0	0	0	0	1	0	0	1	0	0
1	0	0	0	1	1	0	0	1	0	0
0	0	0	0	0	0	0	0	1	0	1
1	0	0	0	0	1	0	- 1	-	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	1	0	1
0	0	0	0	0	0	0	0	-	0	1
1	0	1	0	0	1	1	1	1	0	1
0	0	0	ů 0	0	0	0	0	0	0	1
0	0	0	ů 0	0	0 0	0	0	1	0	0
1	0	0	0	0	0	0	1	1	0	0
0	0	0	ů 0	1	ů O	0	0	1	0	0
1	0	0	ů 0	0	ů O	0	1	1	0	0
-	0	0	0	0	0	0	0	-	0	0
1	0	0	1	0	1	0	0	1	1	1
-	0	0	-	0	-	1	1	-	-	1
0	0	0	ů 0	0	0	0	0	1	0	0
1	0	1	0	0	1	0	1	1	0	0
-	0	-	0	0	-	0	0	-	0	0
0	0	0	ů 0	0	ů O	0	0	1	0	1
0	0	0	ů 0	0	1	0	0	1	0	0
0	0	0	0	0	1	0	0	1	0	0
1	0	0	0	0	0	0	1	1	0	0
1	0	0	0	0	0	0	1	1	0	1
0	0	0	0	0	1	0	0	1	0	1
0	0	0	0	0	1	0	0	1	0	1
0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	1	0	0
1	0	0	0	0	1	0	1	1	0	0
1	0	0	0	0	1	0	1 0	1	0	1
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	Valeriana simplicifolia	Viola palustris
	1	1
	1	0
	1	0
	1	0
	1	0
	0	0
	0	0
1       0         0       0         1       0         0       0         0       0         0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0         1       0         0       0         1       0         0       0         1	1	0
0       0         1       0         0       0         0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0         1       0         0       0         1       0         0       0         1	1	0
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	0	0
0       0         0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0         1       0         0       0         1       0         0       0         1	1	0
0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0         1       0         0       0         1       0         0       0         1       0         0       0         1	0	0
0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0         1       0         0       0         1       0         0       0         1       0         0       0         1	0	0
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	0	0
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1	0
1       0         0       0         1       1         0       0         1       0         0       0         0       0         0       0         0       0         1       0         0       0         1	1	0
0       0         1       1         0       0         1       0         0       0         0       0         1       0         0       0         1	1	0
1       1         0       0         1       0         0       0         0       0         1       0         0       0         1	0	0
0       0         1       0         0       0         0       0         1       0         0       0         1	1	1
1       0         0       0         0       0         1       0         0       0         1	0	0
0       0         1       0         0       0         0       0         1	1	0
0       0         1       0         0       0         0       0         1	0	0
1       0         0       0         0       0         1	0	0
0       0         1       0         0       0         1       0           0       0 <td>1</td> <td>0</td>	1	0
0       0         1       0         0       0         1       0         0       0	0	0
1       0         1       0         1       0         1       0         0       0         1       0         0       0         1       0         0       0	0	0
1       0         1       0         0       0         1       0         0       0	1	0
1       0         1       0         0       0         1       0         0       0	1	0
1       0         0       0         1       0         0       0	1	0
0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0	1	0
1       0         1       0         1       0         1       0         0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0	0	0
1       0         1       0         1       0         0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0         0       0	1	0
1       0         1       0         0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0         0       0	1	0
1       0         0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0	1	0
0       0         1       0         1       0         1       0         0       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         1       0         0       0         0       0	1	0
1     0       1     0       1     0       0     0       1     1       1     0       1     0       1     0       1     0       1     0       1     0       0     0	0	0
1 0 1 0 0 0 1 0 1 1 1 0 1 0 1 0	1	0
1 0 0 0 1 0 1 1 1 0 1 0 1 0 1 0	1	0
0     0       1     0       1     1       1     0       1     0       1     0       0     0       0     0	1	0
1 0 1 1 1 0 1 0 1 0 1 0 0 0	0	0
1 1 1 0 1 0 1 0 0 0	1	0
1 0 1 0 1 0 0 0	1	1
1 0 1 0 0 0	1	0
1 0 0 0	1	0
0 0	1	0
	0	0

Supplementary Table 7 - Variance Inflation Factor and test for multicollinearity between biogegraphic predictors (Western Carpathian fens)						
Variables	VIF of the full set of variables	Discarded	VIF of the remained variables			
Age	3.1		2.8			
Island size (Size)	3.1		2.0			
Nearest neighbor distance (NND)	3.2		3.2			
Number of islands in Buffer 1 (NIB1)	1.9		1.9			
Number of islands in Buffer 2 (NIB2)	3.2		3.1			
Distance to the nearest species source (DNSS)	28.3	х	-			
Stepping stone path to the nearest species source (SSP)	100.3	х	-			
Number of stepping stones (NSS)	90.8		2.7			
Largest gap in the stepping stone path (LGSSP)	9.6		3.6			
Target effect (TE)	6.6		5.3			

2 variables from the 10 input variables have collinearity problem: **SSP DNSS** After excluding the collinear variables, the linear correlation coefficients ranges between: min correlation (NSS ~ NIB2): -0.03 max correlation (LGSSP ~ NIB2): -0.74

GLM model after VIF analysis: Fen plant specialist species richness ~ Age + IS + NND + NIB1 + NIB2 + NSS + LGSSP + TE [Poisson (identity)]

Variables	VIE of the full set of variables	Discarded	VIE of the remained variables	
Island size (Size)				
131d110 312E (312E)	11.0		4.1	
Nearest neighbor distance (NND)	1.7		1.6	
Number of islands in Buffer 1 (NIB1)	3.3		1.7	
Number of islands in Buffer 2 (NIB2)	1.6		1.4	
Distance to the nearest species source (DNSS)	15.9	1	5.0	
Stepping stone path to the nearest species source (SSP)	191.8	х	-	
Number of stepping stones (NSS)	127.1	х	-	
Largest gap in the stepping stone path (LGSSP)	16.0		1.4	
Target effect (TE)	10.1		5.0	

2 variables from the 9 input variables have collinearity problem: SSP NSS

After excluding the collinear variables, the linear correlation coefficients ranges between:

min correlation ( LGSSP  $\sim$  NND ): -0.02

max correlation ( TE ~ DNSS ): 0.52

GLM model after VIF analysis: Mountaintop plant specialist species richness ~ IS + NND + NIB1 + NIB2 + DNSS + LGSSP + TE [Poisson (log)]

Variables	VIF of the full set of variables	Discarded	VIF of the remained variables	
Island size (Size)	15.2		1.3	
Nearest neighbor distance (NND)	10.9	x	-	
Number of islands in Buffer 1 (NIB1)	6.7	х	-	
Number of islands in Buffer 2 (NIB2)	3.3	1	1.2	
Distance to the nearest species source (DNSS)	93.8	х	-	
Largest gap in the stepping stone path (LGSSP)	51.8	х	-	
Number of stepping stones (NSS)	96.9	х	-	
Stepping stone path to the nearest species source (SSP)	187.7	x	-	
Target effect (TE)	85.9		1.1	
Target effect (TE) 6 variables from the 9 input variables have collinearity problem: After excluding the collinear variables, the linear correlation coe min correlation ( TE ~ NIB2 ): 0.05	85.9 NND NIB1 DNSS LGSSP NSS SSP fficients ranges between:		1.1	

GLM model after VIF analysis: Outcrops plant specialist species richness ~ IS + NIB2 + TE [GLM family: Quasipoisson (log)]

Supplementary Table 10 - GLM selection and model averaging (Western Carpathian fens)						
Predictor	AICc weights	Std. Avg. Coeff.	Adjusted Standard Error	z value	Pr(> z )	
Island size	1.00	0.38	0.15	2.62	0.01	
Target effect	0.87	-0.53	0.20	2.66	0.01	
Number of stepping stones	0.54	-0.23	0.15	1.57	0.12	
Nearest neighbor distance	0.41	-0.16	0.11	1.44	0.15	
Largest gap in the stepping stone path	0.41	-0.18	0.14	1.30	0.19	
Number of islands in buffer 2	0.21	-0.04	0.16	0.24	0.81	
Number of islands in buffer 1	0.16	0.04	0.11	0.35	0.73	
Age	0.13	0.03	0.15	0.18	0.85	

Supplementary Table 11 - GLM selection and model averaging (Cantabrian mountaintops)						
Predictor	AICc weights	Std. Avg. Coeff.	Adjusted Standard Error	z value	Pr(> z )	
Island size	0.92	0.11	0.03	3.71	<0.01	
Dist. to the species source	0.62	0.06	0.03	1.70	0.09	
Largest gap in the stepping stone path	0.32	0.04	0.03	1.43	0.15	
Number of islands in buffer 1	0.25	0.04	0.03	1.23	0.22	
Target effect	0.20	-0.06	0.10	0.55	0.58	
Number of islands in buffer 2	0.12	-0.02	0.03	0.70	0.48	
Nearest neighbor distance	0.10	0.03	0.03	0.85	0.40	

Supplementary Table 12 - GLM selection and model averaging (Moravian outcrops)							
Predictor	AICc weights	Std. Avg. Coeff.	Adjusted Standard Error	z value	Pr(> z )		
Target effect	0.66	-0.03	0.01	2.47	0.01		
Island size	0.27	0.02	0.01	1.09	0.27		
Number of islands in buffer 2	0.25	-0.01	0.01	1.02	0.31		