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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

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).

Before assessing biodiversity patterns in terrestrial island-like 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 island-like 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
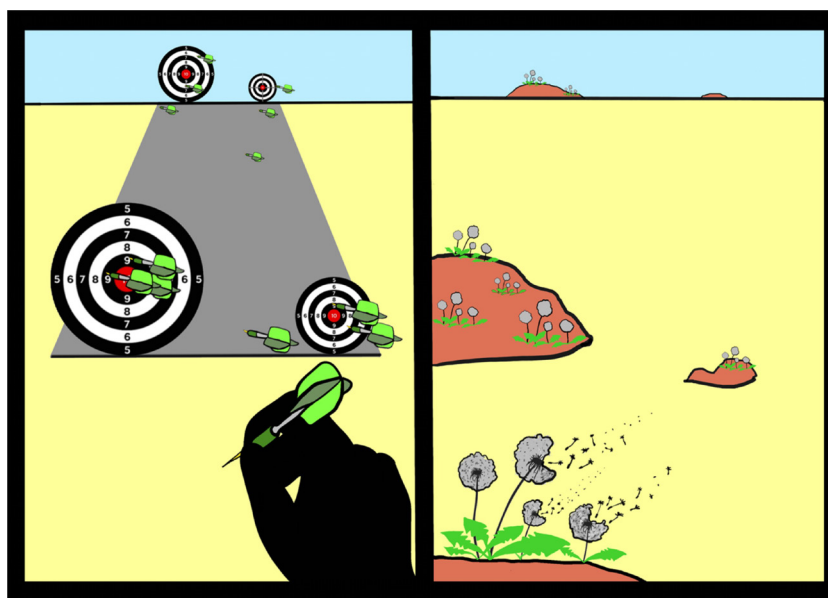

Figure 2. Schematic representation of the target effect. (A) Target effect as an emergent property of multidimensional objects (such as islands) – hitting the target is harder with increasing distance and decreasing size. (B) The target effect applies to both true and edaphic islands because with increasing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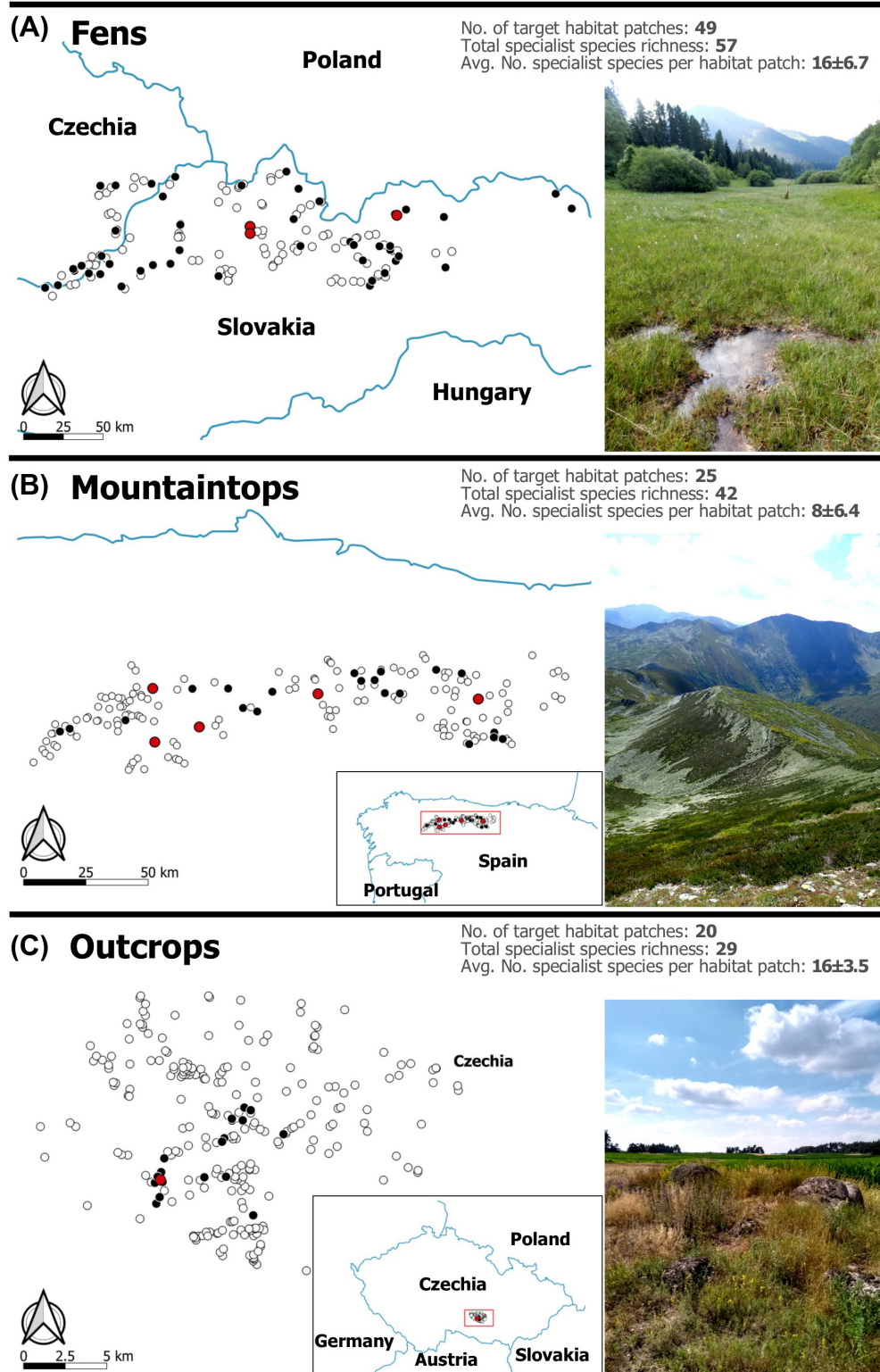
(A) Fens

No. of target habitat patches: **49**
Total specialist species richness: **57**
Avg. No. specialist species per habitat patch: **16±6.7**

Poland

Czechia

Slovakia

Hungary

0 25 50 km

(B) Mountaintops

No. of target habitat patches: **25**
Total specialist species richness: **42**
Avg. No. specialist species per habitat patch: **8±6.4**

Spain

Portugal

0 25 50 km

(C) Outcrops

No. of target habitat patches: **20**
Total specialist species richness: **29**
Avg. No. specialist species per habitat patch: **16±3.5**

Czechia

Poland

Czechia

Germany

Austria Slovakia

0 2.5 5 km

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.

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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 × 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^2) 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 × 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 multi-collinearity 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>).
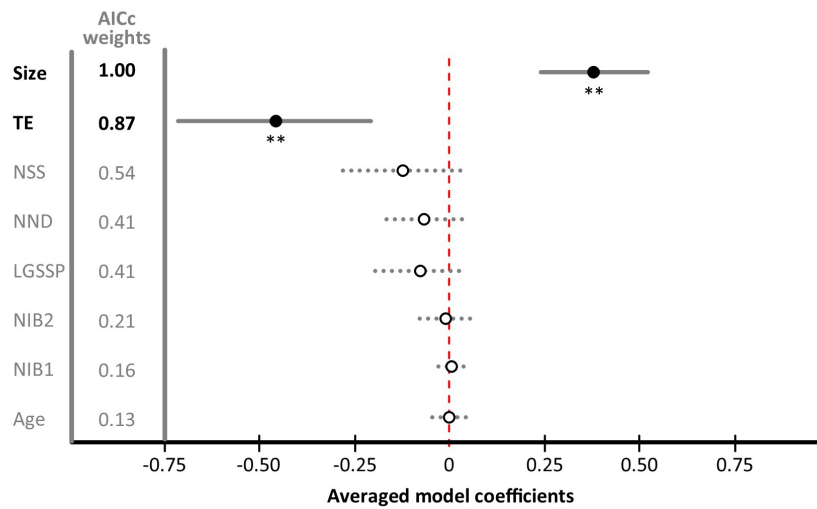
Results
In fens, island size and target effect had the strongest effect on the richness of plant specialists (Fig. 4 and Supporting information). The effect of island size was positive (i.e. larger edaphic islands hosted more specialist species), while the impact of target effect was negative (i.e. fewer 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.
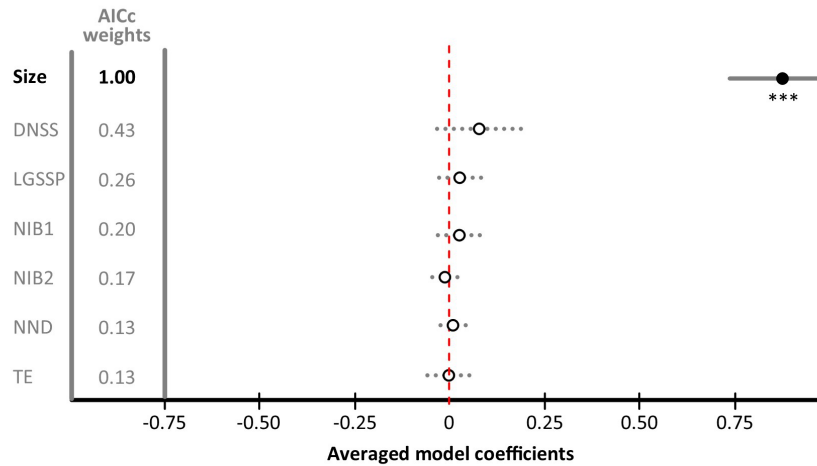
The effect of insularity on edaphic island plants

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.

(A) Fens

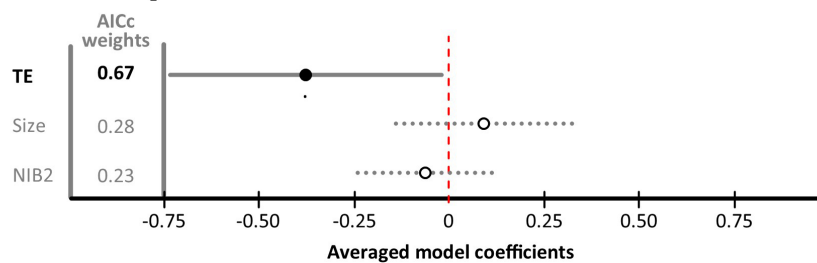## (B) Mountaintops

(C) Outcrops

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 time-consuming 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 (time-since-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.

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

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.05650>.

Data availability statement

All data is provided in the Supporting information.

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