

# Sticking around: Plant persistence strategies on edaphic islands

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## Abstract

**Aim:** Species on islands are at high risk of extinction due to environmental changes, including global warming, land-use alterations and invasions. At local scales, extinctions can be offset by strategies promoting *in situ* persistence. We explored how persistence-related traits of plants—that is, linked to belowground resource conservation, growth, size and longevity—on edaphic islands respond to variation in insularity and the environment (soil and microclimate), including intraspecific variability, which is rarely considered in functional island biogeography. We hypothesised that plants facing strong insularity and harsh soil conditions are characterised by enhanced persistence abilities.

**Location:** Shallow-soil temperate dry grasslands on granite outcrops, Central Europe.

**Methods:** We focussed on edaphic island specialist species belonging to different life histories, namely clonal and non-clonal perennial plants. We used linear and linear mixed-effect models to examine intra- and interspecific trait patterns versus variation in insularity, soil and microclimate.

**Results:** Insularity tended to promote smaller plants (non-clonal species) and belowground resource-conservative strategies (both clonal and non-clonal species), increasing the likelihood of local persistence. Soil also contributed largely to explaining persistence-related trait patterns: plants growing in harsh soil conditions tended to be resource conservative. Clonal species are distinguished by highly consistent responses to variation in insularity and soil conditions, whereas non-clonal plants showed distinct species-specific responses.

**Main conclusions:** Our findings have important implications for the conservation biogeography of edaphic island plant specialists. Clonal species may be susceptible to local extinction should insularity or soil conditions vary, for example, due to abrupt changes in the geographical setting (e.g. habitat loss) or local environmental factors (e.g. N-deposition). Non-clonal species may instead face environmental changes differently; some will go extinct, whereas others will survive, depending on the prevailing

Gianluigi Ottaviani and Francisco E. Méndez-Castro contributed equally to this work.

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abiotic pressures. This seems to challenge previous views that predicted clonal species to be the winners and non-clonal species the losers against local extinction.

#### KEYWORDS

belowground resource conservation, clonality, conservation biogeography, functional island biogeography, intraspecific trait variability, island specialists, longevity, species-specific responses, temperate dry grasslands

## 1 | INTRODUCTION

At the global scale, the rate of species extinction due to environmental changes (e.g. land-use alterations or climate warming) is accelerating at such a pace that the sixth mass extinction has been invoked (Ceballos et al., 2015). At finer scales, this process can translate into the local extinction of species failing to cope with rapid and abrupt changes (Lindborg et al., 2012; Marini et al., 2012; Saar et al., 2012). Still, plant species may avoid or delay local extinction by surviving in favourable microsites or through various strategies that promote in situ persistence outside their optimal environmental conditions (Csörgő et al., 2017; Jiménez-Alfaro et al., 2016). Therefore, studying persistence strategies can improve our understanding of species' extinction risk, which is critical for setting conservation targets.

To thrive successfully in an area under changing environmental conditions, plants must be effective in (i) acquiring, using and conserving resources (Saar et al., 2012); (ii) occupying space through seed establishment and/or clonal spread (Rossetto & Kooyman, 2005) and (iii) recovering after disturbance (Martínková et al., 2020). Functional approaches can assess how these strategies play out under specific environmental conditions (Lavorel & Garnier, 2002; Pérez-Harguindeguy et al., 2013). A good example is provided by temperate grasslands, which harbour many perennial herbaceous species that belong to different life histories and have a variety of persistence strategies (Klimešová, Tackenberg, & Herben, 2016a). A major group of grassland plants comprises clonal species, capable of both sexual and vegetative reproduction. In these species, clonal growth organs such as rhizomes (located belowground, storing buds and carbohydrates) offer the possibility to clonal offspring to explore and occupy new space around the parent plant where resources may be readily available (Janovský & Herben, 2020; Klimešová et al., 2018, 2019). These species coexist with many non-clonal species that rely only on individual plant longevity and regeneration from seeds (Klimešová et al., 2021; Martínková et al., 2020). Both clonal and non-clonal plant species can cope effectively with seasonally cold climates and recurrent disturbances (e.g. mowing and grazing), as typically found in temperate regions. Some of them can also deal with increasingly drier climates, nutrient deposition or altered management regimes (e.g. Fischer et al., 2020). Yet, species that invest more into persistence strategies (e.g. larger and better-protected bud and seed banks, greater clonality) may do better in avoiding or delaying local extinction caused by environmental changes (Lindborg et al., 2012; Saar et al., 2012).

Another critical component in the analysis of persistence strategies is the geographical setting of the study system, such as on islands. These are suitable models because plants under constant isolation should tend to exhibit adaptive persistence strategies to avoid local extinction (MacArthur & Wilson, 1967; Ottaviani et al., 2020; Schrader et al., 2021; Warren et al., 2015; Whittaker et al., 2017). Considering that insular systems (including true oceanic islands and terrestrial habitat islands) constitute or largely contribute to biodiversity hotspots (Cartwright, 2019) and that species on islands are particularly vulnerable to extinctions associated with environmental changes (Macinnis-Ng et al., 2021; Veron et al., 2019), they represent priority elements in conservation biogeography (Richardson & Whittaker, 2010; Whittaker et al., 2005).

Research on plant functional traits in insular systems has boosted in recent years, providing important insights into their eco-evolutionary dynamics (e.g. Biddick et al., 2019; Biddick & Burns, 2021; Burns, 2019; García-Verdugo et al., 2020; Irl et al., 2020; Taylor et al., 2019). Yet, most of this research has focussed on dispersal and resource acquisition traits, neglecting other important functions (e.g. those related to clonality and longevity) that are necessary for a better understanding of how plants may increase their persistence likelihood and therefore possibly offset local extinction (Auffret et al., 2017; Conti et al., 2022). For example, plants occurring on isolated islands experiencing rare immigration and limited gene flow should be characterised by adaptive strategies to persist locally. Under these circumstances, plants should (i) use resources conservatively, hence, grow slowly but live long; (ii) allocate conspicuously into vegetative reproduction and when regenerating sexually, produce few but heavy seeds with limited dispersal and (iii) if clonal, have enhanced ability to occupy space through lateral spread (Ottaviani et al., 2020; Schrader et al., 2021).

Trait-based studies are abundant but are often conducted at the interspecific level because differences amongst species are considered larger than within species (Klimešová et al., 2019; Pérez-Harguindeguy et al., 2013). However, growing evidence shows that intraspecific trait variability can largely contribute to explaining how plants cope with abiotic and biotic changes (e.g. Kichenin et al., 2013; Siefert et al., 2015). Exploring trait patterns at inter- and intraspecific levels may provide additional insights into the persistence strategies of insular species and how they may cope with insularity-related extinction risk and environmental variation.

Our goal in this study is to explore links between persistence-related plant traits at inter- and intraspecific levels and the variation

in insularity and environmental conditions (soil and microclimate) on edaphic islands. These insular systems are defined by patchy distribution in a landscape of discrete bedrock types—such as serpentinite (Harrison, 1997; Kazakou et al., 2008), gypsum (Mota et al., 2003, 2004), dolomite (Miller et al., 2018; Mota et al., 2021), quartz (Eibes et al., 2021; Schmiedel et al., 2015)—or distinct soil conditions, such as shallow, dry and nutrient-poor soils (Mendez-Castro et al., 2021; Ottaviani et al., 2016). Here, we focus on edaphic islands constituted by granite outcrops in Central Europe that host temperate dry grasslands rich in perennial plants specialised in resource-poor shallow soils. Previous studies conducted in the same system have demonstrated the effects of insularity on edaphic islands' specialist species assemblages, namely the decrease in specialist species richness (Mendez-Castro et al., 2021) and the tendency to have fine-tuned strategies to persist in situ (Conti et al., 2022) with increasing insularity. However, it remains poorly understood how persistence-related traits of individual species or species grouped by distinct life histories (i.e. clonal and non-clonal species) respond to changes in insularity, soil and microclimate conditions. This is an important gap because responses at the assemblage level may be formed by different, if not contrasting, patterns at the intra- and interspecific levels (Kichenin et al., 2013).

Given the geographical setting and special edaphic conditions, we expect insularity and soil to play a major role in shaping traits related to the local persistence of edaphic island plant specialists, whereas microclimate to have less influence. Specifically, we hypothesise that:

(H1) Insularity promotes enhanced plant persistence strategies, namely with stronger insularity, plants should tend to use resources more conservatively, grow more slowly but live longer and, if clonal, have a greater ability to occupy space.

(H2) Harsh soil conditions (resource-poor shallow soils) also promote enhanced plant persistence strategies—with similar predictions as for insularity.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and focal species of edaphic islands

We selected 20 granite outcrops in the southern Czech Republic, located at elevations of around 450 m a.s.l. (centroid: 49°14'12"N, 15°57'26"E; Figure 1). These outcrops (edaphic islands) are scattered across an area of approximately 100 km<sup>2</sup> and embedded in an agricultural landscape. Their average area is 2912 m<sup>2</sup> (min = 361 m<sup>2</sup>, max = 14,115 m<sup>2</sup>). The regional macroclimate is temperate (mean annual temperature: 6.5–8°C, annual precipitation: 500–550 mm), characterised by marked temperature and precipitation seasonality (Doležal et al., 2022). The vegetation growing on these gently dome-shaped outcrops (maximum elevation ~5–10 m compared to the surrounding area) is acidophilous dry grassland.

We focussed on 13 perennial plant species confined to the outcrop grasslands. These species constitute ~45% of the total number

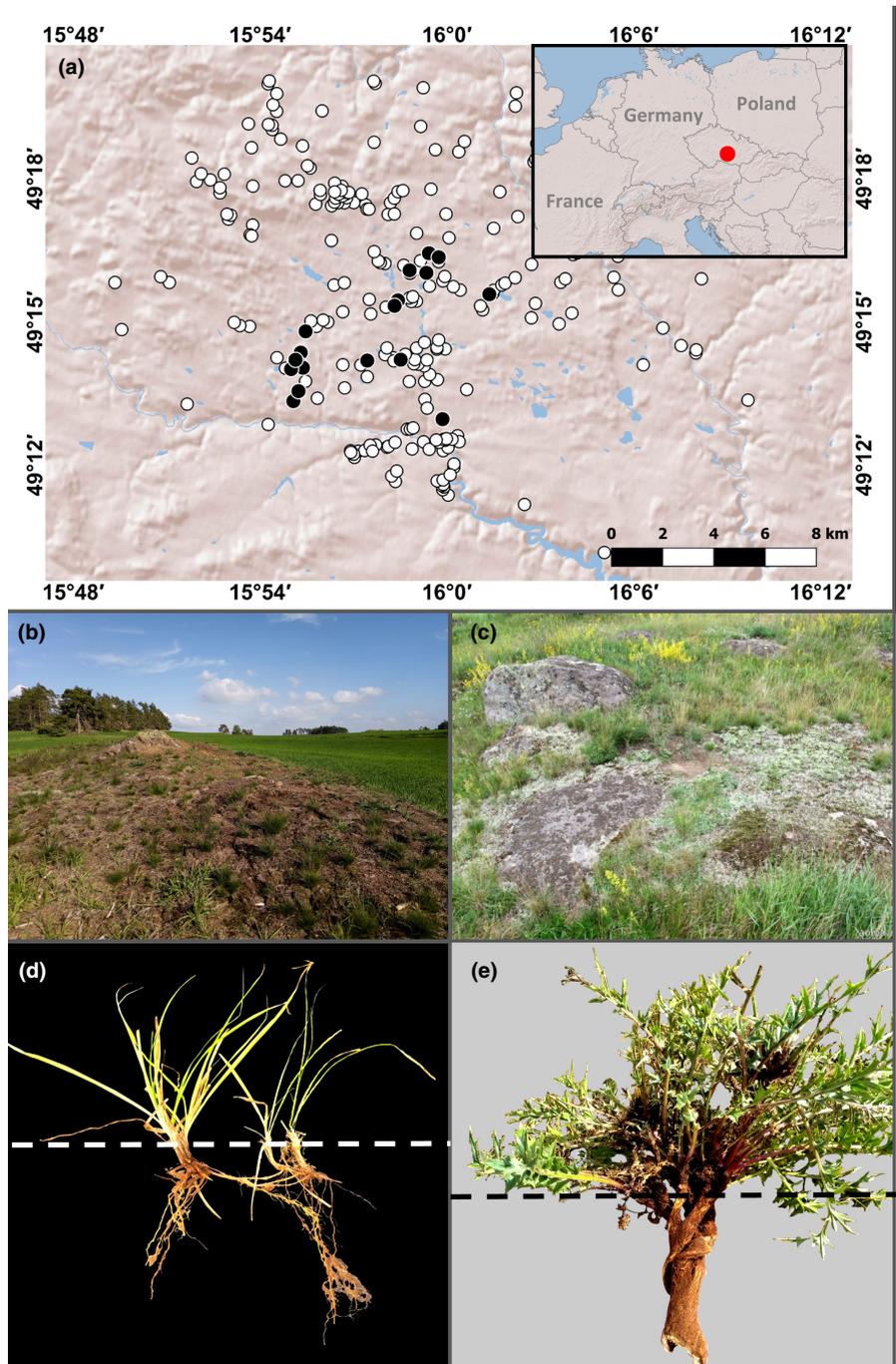
of specialists of this vegetation type (Mendez-Castro et al., 2021)—we could not sample the other species because they either occurred on fewer than five edaphic islands or their conservation status would not allow the destructive sampling required for collecting the selected persistence-related traits. Edaphic island specialists are considered to be: (1) adapted to the harsh habitats of rocky outcrops (especially in relation to resource-poor shallow soils; Doležal et al., 2022) and (2) more affected by insularity than non-specialists (for which edaphic patches should not constitute an island), that is, the surrounding landscape should represent an effective barrier to dispersal and establishment, similar to water for oceanic islands (Conti et al., 2022; Mendez-Castro et al., 2021). The 13 species belong to different plant functional types (nine forb, two chamaephytes, one grass and one sedge species), life histories (five clonal, eight non-clonal species; Figure 1) and nine families. The clonal species are *Carex caryophyllea*, *Cerastium arvense*, *Hieracium pilosella*, *Koeleria macrantha* and *Trifolium alpestre*, whereas the non-clonal species are *Carlina acaulis*, *Centaurea stoebe*, *Helianthemum grandiflorum* subsp. *obscurum*, *Knautia arvensis*, *Lychnis viscaria*, *Scleranthus perennis*, *Silene nutans* and *Thymus pulegioides*. Hereafter, we refer to these species by their genus name. All species were found on most of the edaphic islands (12 to 20 islands), except for *Helianthemum* and *Carex* (on six islands).

### 2.2 | Persistence-related plant traits

We sampled three well-developed and healthy individual plants per species on each edaphic island (total sample size = 538; only in a few cases, we could sample two individuals because of small population size). The sampling was performed at the peak of the vegetative and flowering phenological phase in the spring and summer 2019. Trait-data collection and measurement procedures followed standard protocols (Klimešová et al., 2019; Pérez-Harguindeguy et al., 2013). We measured seven traits related to local plant persistence (Table 1). In the field, we measured plant height and lateral spread (maximum distance between rooting units connected through rhizomes and/or stolons; for clonal species only). For the other five traits, we collected plant material in the field that was later processed in the laboratory. For Belowground organ Dry Matter Content (BDMC), a ~2-cm long portion of rhizome (for clonal species) or tap root (for non-clonal species) was cut. The fresh weight was recorded. Then, the plant material was oven-dried at 60°C for 72 h and the dry weight was measured. BDMC was calculated as the ratio between the oven-dried and fresh mass weight (as for leaf dry matter content (LDMC); Pérez-Harguindeguy et al., 2013).

Anatomical traits—age, radial growth, storage tissue and vessel size (Table 1)—were measured for non-clonal plants only (346 individuals analysed across all species). We did not collect anatomical traits for clonal species because the oldest part of the rhizome is often inaccessible or decomposed. In the field, we cut a ~2-cm long portion located between the root and stem system from each sampled individual. This is the oldest plant part present in the

**FIGURE 1** (a) Map and geographical location of the studied edaphic islands on granite outcrops in the Czech Republic, Central Europe (red circle in the inset); black circles correspond to the studied edaphic islands, whereas the white circles represent all edaphic islands in the surrounding landscape. (b) Example of an edaphic island embedded in the agricultural landscape. (c) a close-up of the studied temperate dry grassland on shallow soils. Examples of two specialist species of edaphic islands, showing their aboveground and belowground structures (dashed line indicates approximate ground surface): (d) the clonal *Carex caryophyllea* with rhizomes connecting two rooting units and (e) the non-clonal *Carlina acaulis* with a conspicuous tap root. Photo credit: Francisco E. Méndez-Castro



studied growth forms that allow estimation of plant age (Klimešová et al., 2019). These plant materials were preserved in 50% ethanol and once in the laboratory, sectioned using a sledge lab-microtome, with thickness between 15 and 40  $\mu\text{m}$ . Cross-sections were then double stained using a mixture of Astra blue and safranin dye, dehydrated (using a series of solutions with different ethanol concentrations), washed with xylene and fixed on slides with Canada balsam. These slides were examined using a microscope. The ImageJ software (Schneider et al., 2012) was used to evaluate the number of annual rings (age), mean annual increments (radial growth), percentage of storage tissue (parenchyma) and maximum vessel size in the cross-section.

### 2.3 | Insularity, soil and microclimate variables

We used the target effect metric as a proxy of insularity. This is calculated as the natural logarithm of the ratio between the distance of the target island and its putative species source—that is, the largest and specialist-richest island(s) considering those patches scoring above the 75th percentile of the data distribution of specialist richness and island size—and the square root of its area (see Méndez-Castro et al., 2021 for more details). High values of the target effect imply that islands are difficult to colonise because of their small size and/or far location from the species source. In the study system, the target effect effectively captures different dimensions of insularity,

**TABLE 1** Name (in italics, indicating whether the trait was collected for clonal, non-clonal species or both), definition (with variable type and units), major plant functions and key references of the persistence-related traits included in this study

Trait name	Definition (variable type and units)	Function	Key reference
<i>Plant height</i> [Clonal, Non-clonal]	Maximum plant height (continuous; cm)	Vertical space occupancy	Pérez-Harguindeguy et al. (2013)
<i>Belowground organ Dry Matter Content (BDMC)</i> [Clonal, Non-clonal]	Tissue density of belowground organs, for example, taproots, rhizomes (continuous; mg g <sup>-1</sup> )	Resource conservation (mainly water); Structural support	de Bello et al. (2012)
<i>Lateral spread</i> [Clonal]	Maximum distance between offspring and the parental individual in clonal plants (continuous; cm year <sup>-1</sup> )	Horizontal space occupancy; Vegetative reproduction	Klimešová et al. (2019)
<i>Age</i> [Non-clonal]	Maximum plant age measured at the root collar (continuous; year)	On-spot persistence	Klimešová et al. (2019)
<i>Radial growth</i> [Non-clonal]	Average annual increment measured at the root collar (continuous; μm)	On-spot persistence; Resource use	Klimešová et al. (2019)
<i>Storage tissue</i> [Non-clonal]	Proportion of storage tissue measured at the root collar (continuous; %)	Resource conservation; Recovery after damage	Klimešová et al. (2019)
<i>Vessel size</i> [Non-clonal]	Cross-sectional maximum vessel diameter measured at the root collar (continuous; μm <sup>2</sup> )	Transport capacity; Resistance to frost and drought	Klimešová et al. (2019)

namely isolation, area, landscape configuration and connectivity (Appendix S1: Figure 4a, b). The target effect (dimensionless) was calculated for each edaphic island.

We collected 38 soil samples on 17 edaphic islands (2–3 per island, depending on its area) located near the microclimatic stations (see below). We were unable to sample all the 20 outcrops due to logistic constraints. Each sample contained ~100g of soil. To determine soil nutrient status, we measured eight parameters, namely pH, organic matter, electrical conductivity, total nitrogen, ammonium, nitrate, total phosphorus and exchangeable phosphorus (see Appendix S1: Methods S1 for details on analytical procedures). For soil textural parameters, we measured clay, silt and sand content based on particle size (clay: 0.1–2 μm; silt: 2–50 μm; sand: 50–2000 μm; Appendix S1: Figure S2). We also measured soil depth at each sampled plant individual.

We gathered information on 18 microclimate variables using 38 automatic data logger stations (TOMST) which was recorded at 10 cm aboveground and 10 cm belowground every 15 minutes for 1 year (July 2019–July 2020). We placed two to three stations on each of the 17 outcrops to capture microclimatic variability associated with the fine-scale topographic heterogeneity provided by the edaphic island. The collected variables relate to temperature and moisture, which can strongly influence plant growth and establishment dynamics (Doležal et al., 2022), namely: the mean annual value and coefficient of variation (CV) of air temperature, soil temperature and moisture; minimum and maximum values of air temperature, soil temperature and moisture during the growing season (April

to October) and outside the growing season (November to March) (Appendix S1: Figure S3).

## 2.4 | Data analyses

We used the interpolation procedure proposed by Husson and Josse (2016) to impute soil and microclimate data for the three missing edaphic islands. Soil parameters were aggregated into four ecologically meaningful predictors representing different dimensions of edaphism: (1) fertility (informing on soil nutrient status), (2) sandiness index (related to soil texture and dryness), (3) mean depth (proxy for the possibility of rooting and acquiring resources in the soil profile and for soil resource availability) and (4) depth coefficient of variation (CV; estimate of soil resource heterogeneity). Soil fertility was identified as the first axis of a Principal Component Analysis (PCA; the first axis explained ~49% of the variance, with positive scores associated with more fertile soils; Appendix S1: Figure S5) performed on the eight soil nutrient variables. The sandiness index was calculated from the textural variables as  $\sum \text{sand} / \sum (\text{silt} + \text{clay})$ , that is, higher sand proportion resulted in higher values of this index, implying lower water retention capacity. Mean soil depth and CV were calculated at the island level using all measurements taken on each island (five soil depth measurements per sampled individual/species/island = total > 2500 measurements). Regarding microclimate, we ran a PCA on the 18 variables and selected the first two axes as predictors in the models. Specifically, the first PCA axis was

positively related to the annual mean of air and soil temperature and negatively to the seasonality of these variables (PC1clim, explaining ~29% of the variance). The second PCA axis was positively related to annual mean soil moisture and less extreme soil temperatures (PC2clim; explaining ~24% of the variance; Appendix S1: Figure S3). Trait values were averaged (using the three values/species/island) for each species at the edaphic island scale.

Before running the models, we controlled for collinearity amongst the seven insularity, soil and microclimate variables using Spearman's rho correlation coefficient (with Bonferroni correction) and detected no issues (Appendix S1: Table S6). We first ran Linear Mixed-effect Models (LMMs) for clonal and non-clonal species separately (i.e. for each life history; responses at the interspecific level). In the LMMs, we set the species trait average at the island scale as the response variable, insularity (target effect) and environmental (soil and microclimate) variables as predictors (i.e. fixed effects; scaled and centred) and treated species identity as a random effect (informing on the magnitude of species-specific responses). The variance explained by fixed effects alone (marginal  $R^2$ ) and by fixed and random effects together (conditional  $R^2$ ) was calculated. Because, we aimed at gaining insights into intraspecific responses to insularity, soil and microclimate (and because this study had an inherent explorative component), we examined the associations at the level of single trait versus single predictor. We used bivariate Ordinary Least Squares (OLS) linear models, setting species identity as a grouping factor (interacting with the single predictor). We identified important relationships based on the model coefficient and its 95% confidence intervals (direction and robustness of the relationship),  $R^2$  (goodness of fit and strength of the relationship) and  $p$ -value (significance of the relationship). Except for storage tissue, all other traits required log-transformation to accommodate linearity and normality of data distribution and homoscedasticity of model residuals, whereas predictors did not require transformation. For clonal and non-clonal species separately, we visualised the multivariate trait space identified by persistence-related traits and the species occupancy in this functional space using Non-metric Multidimensional Scaling (NMDS). As traits were measured in different units, we used Gower distance in the NMDS and set 100 random starts and two dimensions. We conducted all the analyses in R version 4.0.1 (R Core Team, 2020) using functions from the packages *missMDA* (for PCA; Husson & Josse, 2016), *vegan* (for NMDS; Oksanen et al., 2019), *lme4* (for LMM; Bates et al., 2015) and *smatr* (for OLS; Warton et al., 2012).

### 3 | RESULTS

Insularity, represented by the target effect, was positively related to BDMC in clonal and non-clonal plant species, whereas negatively associated with plant height in non-clonal plants (Table 2). Soil depth mean and CV were positively associated with vessel size. PC1clim (informing on annual air and soil temperatures and their seasonality) was negatively related to plant height and positively to

BDMC in clonal species. PC2clim (related to soil moisture and soil temperature extremes) was marginally positively associated with BDMC of non-clonal species. Except for BDMC of clonal species—where fixed effects accounted for 58% and no variance was explained by the random effect “Species identity”—predictors alone generally explained only a small proportion of the variability in the models (marginal  $R^2$  between 1% and 4%) (Table 2). Most of the model variability was explained by the random effect (conditional  $R^2$  up to 93%; Table 2).

Clonal species (except for *Koeleria*, which is distinguished by consistently taller individuals and *Carex* by higher BDMC) showed greater overlap in the multifunctional NMDS space defined by persistence-related traits than non-clonal species, which were instead characterised by distinct and species-specific occupancies (Figure 2a,b).

When considering the links between single traits and single predictors for clonal species, the variance explained by predictors ranged between 17% and 65% for the most important relationships (Table 3). The most consistent relationships were found for target effect and soil depth CV with BDMC, which exhibited strong positive links across all species. Plant height and lateral spread were found to be less related to insularity, soil and microclimate (Table 3).

Amongst the non-clonal species, *Carlina*, *Helianthemum*, *Lychnis* and *Scleranthus* were tightly related to changes in insularity, soil and microclimate, whereas *Silene* and *Thymus* responded weakly. The variance explained by single predictors in the OLSs for the most important relationships ranged between 15% and 87% (Table 4). The most responsive traits across species were radial growth and storage tissue. Consistent trait-environment patterns were identified in only a small proportion of species (two or three). The majority of trait-environment (soil and microclimate) links were highly species- and predictor specific, either unique to some species or sometimes contrasting within the same single trait-single predictor relationship (Table 4).

### 4 | DISCUSSION

We found general support for our fundamental expectation: insularity and soil played a major role in shaping persistence-related traits of edaphic island plant specialists. Plants in more insular settings and harsher soil conditions were characterised by resource-conservative strategies, with trait values indicative of enhanced ability to persist locally. However, predictors explained only small portions of the variability in the models, except for BDMC in clonal species. Most of the explained variability was instead related to species identity (Table 2). This finding suggests that strategies to persist *in situ* can vary widely amongst plant species. However, the consistency of trait responses to insularity, soil and microclimate differed largely between the two life histories. Clonal species showed highly consistent trait patterns with overlaps in their persistence strategies, whereas non-clonal species exhibited species-specific trait patterns and distinct persistence strategies (Figure 2).

TABLE 2 LMM results for the clonal and non-clonal species. Sign (arrow direction), significance ( $p$ -value: \*\*  $\leq .01$ ; \*  $\leq .05$ ;  $\leq .1$ ) and strength ( $R^2$  values) of the relationship are reported. Only the most important relationships are indicated (see Appendix S2 for all model summary statistics)

Trait	Fixed effects							Random effect	
	Insularity	Soil				Microclimate		$R^2$ marginal	Species ID
	Target effect	Fertility	Sandiness	Depth mean	Depth CV	PC1clim	PC2clim		$R^2$ conditional
<b>Clonal species</b>									
Plant height	-	-	-	-	-	↓*	-	0.01	0.90
BDMC	↑*	-	-	-	-	↑**	-	0.58	0.58
Lateral spread	-	-	-	-	-	-	-	0.01	0.83
<b>Non-clonal species</b>									
Plant height	↓**	-	-	-	-	-	-	0.03	0.86
BDMC	↑*	-	-	-	-	-	↑.	0.04	0.75
Age	-	-	-	-	-	-	-	0.01	0.90
Radial growth	-	-	-	-	-	-	-	0.01	0.88
Storage tissue	-	-	-	-	-	-	-	0.01	0.71
Vessel size	-	-	-	↑**	↑**	-	-	0.02	0.93

#### 4.1 | Clonal and non-clonal edaphic island plants have different persistence strategies

Except for plant height and BDMC, we assessed different traits for clonal and non-clonal species. Yet, all the selected traits included in this study are associated with different functions shaping the local persistence of species. These are: (1) belowground resource conservation represented by BDMC and storage tissue; (2) plant growth and size associated with plant height, lateral spread, radial growth and vessel size; and (3) plant longevity (age). However, not all traits were found to respond similarly to variation in insularity and the environment (soil and microclimate). BDMC emerged as the most responsive and consistent trait across species, especially in clonal plants (58% of model variability explained and no effect on species identity; Table 2). This trait is linked to resource conservation (mainly water) and structural support of coarse belowground organs. It can also provide insights into plant ability to overwinter and multiply clonally (de Bello et al., 2012). BDMC may serve as a surrogate for other belowground traits and functions that are more laborious to measure (e.g. anatomical traits), yet its functional role and relationships with other traits and along different gradients (e.g. elevation) should be examined.

Clonal species consistently exhibited similar responses to insularity and environmental conditions (in this case mainly soil). In temperate grasslands, clonal species tend to prefer moist and nutrient-rich soils (Klimešová et al., 2018). Therefore, clonal plant specialists of the dry, sandy, shallow and nutrient-poor soils of granite outcrops may occupy, thanks to their enhanced longevity and reduced growth, one of the limits of their ecological niche in the temperate grassland biome. However, we cannot fully support this inference by direct age estimation because we lack such measures for clonal plants.

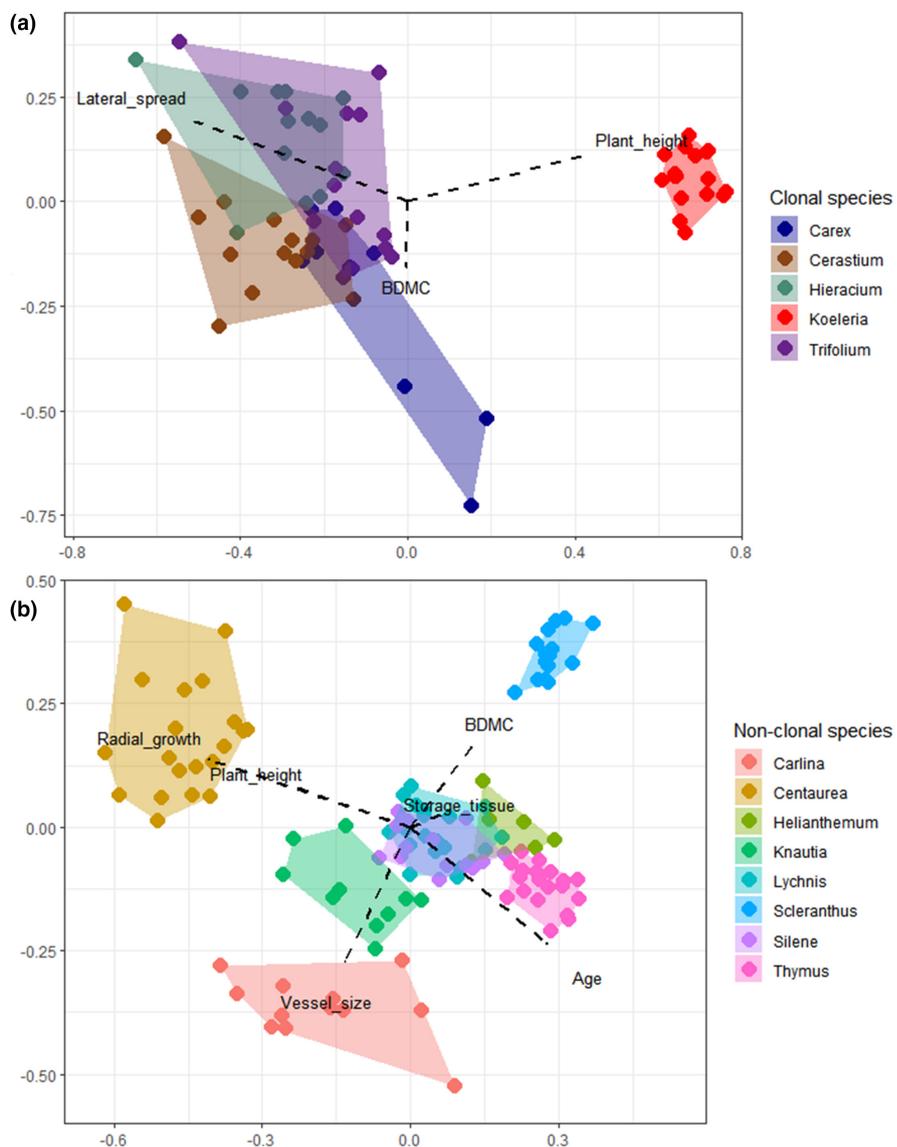
Yet, demographical studies show that these species can exceed the lifespan of non-clonal plants (Janovský & Herben, 2020) and persist in remnant populations (Jiménez-Alfaro et al., 2016; Lindborg et al., 2012; Marini et al., 2012; Saar et al., 2012).

A quite different scenario emerged for non-clonal species. Half of these species (*Carlina*, *Helianthemum*, *Lychnis* and *Scleranthus*) responded strongly to variation in insularity, soil and microclimate, with some species more strongly related to insularity (*Lychnis*), whereas others more strongly related to soil conditions (and to a lesser extent to climate; *Helianthemum*). In contrast, the other half of the species, especially *Silene* and *Thymus*, were only weakly or not affected by variation in insularity and the environment. Trait responses also showed no associations with plant functional types. For example, the chamaephytes *Helianthemum* and *Thymus* or the forbs *Carlina*, *Centaurea*, *Knautia* and *Scleranthus* were distinguished by well-differentiated species-specific persistence strategies (Figure 2b). This could be due to differences in rooting depth and regenerative strategies rather than plant longevity (see also Doležal et al., 2022). In *Knautia*, local persistence seems to be fostered by a reduced growth in more insular and heterogeneous soil conditions. Such a variable- and species-specific set of responses may indicate that (at least some of) the non-clonal species are likely well adapted and not limited by the distinct biogeographical and ecological conditions of the spatially confined temperate dry grasslands on granite outcrops.

#### 4.2 | Trait-insularity links: Edaphic islands can operate as true islands, especially for clonal species

Plant species on more insular edaphic islands tended to be more resource conservative in their belowground organs. Moreover, smaller

**FIGURE 2** NMDS for (a) clonal and (b) non-clonal species in the space defined by persistence-related traits. Stress values (0.029 for clonal species, 0.127 for non-clonal species) indicate a good fit of the two-dimensional scaling



**TABLE 3** OLS regression results for the five clonal species. Sign (arrow direction), significance ( $p$ -value: \*\*  $\leq .01$ ; \*  $\leq .05$ ;  $\leq .1$ ) and strength ( $R^2$  values) of the relationship are reported. Only the most important relationships are indicated (see Appendix S2 for all model summary statistics). The minimum and maximum trait values are reported in squared brackets (see Table 1 for units)

Species	Trait <sub>[min-max]</sub>	Target effect	Soil				Microclimate	
			Fertility	Sandiness	Depth mean	Depth CV	PC1clim	PC2clim
Carex	BDMC <sub>[843-961]</sub>	↑* 0.57	↑** 0.65	↓* 0.50	↓* 0.61	↑* 0.50	-	↑* 0.44
Cerastium	BDMC <sub>[804-962]</sub>	↑** 0.46	-	-	-	↑** 0.44	-	-
Hieracium	Plant height <sub>[8-22]</sub>	-	-	-	-	-	↓** 0.47	-
	BDMC <sub>[765-962]</sub>	↑* 0.46	-	-	-	↑* 0.39	↑ 0.26	-
Koeleria	Lateral spread <sub>[11-34]</sub>	-	-	-	-	↑ 0.30	-	-
	Plant height <sub>[44-65]</sub>	-	↑ 0.17	-	-	-	-	-
	BDMC <sub>[780-965]</sub>	↑** 0.42	-	↓* 0.26	↓ 0.19	↑ 0.21	-	-
Trifolium	Lateral spread <sub>[1-2]</sub>	-	-	↑ 0.20	-	-	↑* 0.33	-
	Plant height <sub>[12-27]</sub>	-	↓ 0.24	-	-	-	-	-
	BDMC <sub>[774-697]</sub>	↑* 0.44	↑ 0.26	-	↓* 0.38	↑* 0.38	-	-
	Lateral spread <sub>[6-31]</sub>	-	-	↓ 0.22	-	-	-	-

TABLE 4 OLS regression results for the eight non-clonal species. Sign (arrow direction), significance ( $p$ -value: \*\*  $\leq .01$ ; \*  $\leq .05$ ;  $\leq .1$ ) and strength ( $R^2$  values) of the relationship are reported. Only the most important relationships are indicated (see Appendix S2 for all model summary statistics). Minimum and maximum trait values are reported within squared brackets (see Table 1 for units)

Species	Trait <sub>[min-max]</sub>	Insularity	Soil				Microclimate	
		Target effect	Fertility	Sandiness	Depth mean	Depth CV	PC1clim	PC2clim
<i>Carlina</i>	Plant height <sub>[14-24]</sub>	-	↓ 0.27	↑ 0.26	-	-	-	-
	BDMC <sub>[351-692]</sub>	-	-	-	-	-	-	↑* 0.44
	Age <sub>[5-20]</sub>	-	↑ 0.31	-	-	-	-	-
	Radial growth <sub>[242-1094]</sub>	-	↓ 0.31	↑ 0.30	↑** 0.57	↓ 0.28	-	-
	Storage tissue <sub>[57-73]</sub>	↑* 0.35	↑* 0.38	-	↓ 0.29	↑* 0.50	-	-
<i>Centaurea</i>	Storage tissue <sub>[5-48]</sub>	-	-	↑* 0.27	↑ 0.15	-	-	-
	Vessel size <sub>[499-1407]</sub>	-	-	↑* 0.28	-	-	-	-
<i>Helianthemum</i>	Plant height <sub>[18-21]</sub>	-	-	-	-	-	↑* 0.71	-
	BDMC <sub>[745-928]</sub>	-	-	↓* 0.73	-	-	-	-
	Age <sub>[11-20]</sub>	-	↑* 0.82	-	-	-	-	-
	Radial growth <sub>[175-340]</sub>	-	-	↑* 0.68	↑* 0.71	-	-	-
	Storage tissue <sub>[14-45]</sub>	-	-	-	-	-	↓ 0.54	-
	Vessel size <sub>[323-618]</sub>	-	-	↑** 0.87	-	-	-	-
<i>Knautia</i>	Radial growth <sub>[202-620]</sub>	↓** 0.61	↓* 0.44	-	-	↓* 0.40	-	-
	Vessel size <sub>[1014-1919]</sub>	-	-	-	-	-	↑* 0.43	-
<i>Lychnis</i>	Plant height <sub>[11-48]</sub>	↓* 0.22	-	-	-	-	-	-
	BDMC <sub>[735-961]</sub>	↑* 0.30	-	-	-	-	-	-
	Age <sub>[8-17]</sub>	↓* 0.25	-	-	-	-	-	-
	Radial growth <sub>[156-285]</sub>	-	-	-	-	↑** 0.34	-	-
	Storage tissue <sub>[42-67]</sub>	-	-	-	-	-	-	↑ 0.16
<i>Scleranthus</i>	Vessel size <sub>[457-1070]</sub>	-	-	↑ 0.16	-	-	↑* 0.29	-
	BDMC <sub>[800-996]</sub>	↑** 0.47	↑* 0.28	↓* 0.30	-	-	-	-
	Age <sub>[2-3]</sub>	-	-	-	-	-	↑* 0.27	-
	Radial growth <sub>[115-203]</sub>	-	↑ 0.23	-	-	-	-	-
<i>Silene</i>	Storage tissue <sub>[36-61]</sub>	↑ 0.21	-	-	-	-	-	-
	Plant height <sub>[12-49]</sub>	↓** 0.46	-	-	-	-	-	-
<i>Thymus</i>	Plant height <sub>[9-17]</sub>	-	-	-	-	↑* 0.25	-	-

non-clonal plants were favoured by stronger insularity (Biddick et al., 2019; Biddick & Burns, 2021; Burns, 2016). Both trends suggest enhanced persistence ability (Ottaviani et al., 2020; Schrader et al., 2021). Smaller plants with the ability to store resources in belowground organs such as taproots or rhizomes may indicate adaptive strategies aimed at less costly economics (Lindborg et al., 2012; Saar et al., 2012). Amongst the non-clonal species, *Lychnis* and *Scleranthus* were the most responsive to variation in insularity, suggesting that these species may be highly affected by alterations in the biogeographical setting, such as a reduction in connectivity due to habitat loss.

Evidence that clonal species are more resource conservative with increasing insularity, both intra- and interspecifically, offers insights into their ecology and conservation biogeography. Consistently denser belowground organ tissues of rhizomes may imply that the studied clonal species tended to be more resource conservative

and therefore longer lived (Klimešová, Nobis, & Herben, 2016b) in more insular sites. It also suggests that rooting units forming a clone can be connected for longer periods, possibly uptaking and sharing resources over larger areas. Such an integrated strategy may constitute the most effective way for clonal plants to survive in more insular and resource-limited environments ("grow slow-live long" strategy; Jónsdóttir & Watson, 1997). Additionally, clonal species are known to be poor seed producers (Herben et al., 2015) and a trade-off between local persistence and dispersal (Rossetto & Kooyman, 2005) may limit their ability to reach distant or tiny islands of suitable habitat. Dispersal of clonal species may, therefore, rely on well-connected edaphic islands linked by closely located steppingstones. Yet, once these species arrive and establish on new islands, their persistence can be supported by the production of clonal growth organs (e.g. rhizomes), which may also serve for resource storing, foraging and sharing (Jónsdóttir & Watson, 1997; Klimešová

et al., 2018). All these strategies may increase the likelihood of clonal plants to persist locally and thus reduce their insularity-related extinction risk. However, lateral spread of clonal species showed no relationships with insularity and very sparse, inconsistent links with soil and microclimate. This seems to contrast with the results obtained when all clonal specialist species were analysed at the insular assemblage level (based on interspecific differences; Conti et al., 2022). In that case, the lateral spread was positively associated with insularity; this suggests that the response at the assemblage level is formed by different, or lack thereof, responses at the species level (Kichenin et al., 2013). Alternatively, this could be a sampling effect because we were able to collect trait data for approximately half of all clonal specialists.

### 4.3 | A strong effect of soil and weak microclimate impact on persistence strategies of edaphic island plants

The studied edaphic islands on granite outcrops are distinguished by shallow soils with high sand content, low water retention capacity and limited nutrient availability. These harsh edaphic conditions have contributed greatly to shaping the trait patterns that can influence the local persistence of specialised perennial plant species, which should be fine-tuned to cope with these abiotic constraints (Cartwright, 2019; Damschen et al., 2012). Evidence that soil is one of the key drivers of persistence strategies of edaphic island plants aligns with other studies (e.g. Hulshof & Spasojevic, 2020; Kazakou et al., 2008). The mean soil depth influenced BDMC patterns of clonal plants (with evidence of more resource-conservative strategies in shallower soils in three species), yet this effect was weaker and less consistent than that revealed for soil depth variability, which is a proxy for fine-scale soil heterogeneity. Increasing variability in soil depth was indeed consistently related to higher BDMC values across all clonal species, suggesting that fine-scale soil heterogeneity causes these plants to be more conservative belowground—a possibly adaptive “stay where you are” strategy (Graae et al., 2018).

Non-clonal plants grew better in deeper and sandier soils, whereas plants on more fertile soils tended to grow older but more slowly, as in *Carlina* and *Helianthemum*. These findings challenge the notion that plants in harsher environments should grow slower and live longer (Nobis & Schweingruber, 2013). *Carlina* and *Helianthemum* may have unique strategies at the intraspecific level to successfully persist in the distinct soil conditions of edaphic islands, which do not necessarily constrain their growth. Non-clonal plants also showed a greater ability to transport water through larger vessels in deeper, more variable and sandier soils. This may be explained by an adaptive functional trade-off between hydraulic safety and efficiency (Drake et al., 2015). Larger vessels may lead to faster growth (as in *Helianthemum*, likely facilitated by its deep rooting ability; Doležal et al., 2022) and higher evapotranspiration. At the same time, this strategy may also increase the risk of embolism associated with

frequent cold and arid spells characteristic of highly seasonal temperate dry grasslands—extreme events that are expected to be exacerbated by global climate change (Coumou & Rahmstorf, 2012).

Microclimate affected only few traits; still, clonal plants under warmer and drier conditions tended to be more resource conservative and smaller (Ottaviani & Keppel, 2018). Overall, however, we have revealed inconsistent patterns amongst life histories and species. This may flag a minor role of microclimate in shaping the local persistence of edaphic island plants compared to insularity and soil. The regional macroclimate can be considered the same across all the studied edaphic islands. Microclimate instead (recorded by data loggers) can differ within a single island due to differences in slope aspect, inclination and solar radiation resulting from the rugged terrain and dome-shaped topography of the outcrops. However, this fine-scale climate heterogeneity appears to have exerted limited influence on the persistence-related trait patterns of the edaphic island plant specialists—probably because these outcrops do not represent conspicuous elements in the landscape, as in the case of inselbergs distinguished by high elevation, topographic complexity and habitat diversity where microclimate can play a prevalent role in modulating species distribution, persistence and trait patterns (De Smedt et al., 2018; Ottaviani et al., 2016). Alternatively, the lack of effect may be a consequence of delayed plant responses to climate fluctuations (Evers et al., 2021).

### 4.4 | Implications for conservation

Plant species specialised to edaphic islands are considered to be more resistant to environmental changes (Harrison, 1997). The extinction risk associated with environmental changes (e.g. climate warming, land-use alterations and invasion) of these soil specialists should, therefore, be lower than that of species preferring milder edaphic conditions (Damschen et al., 2012). However, findings are discrepant because environmental changes may also alter landscape configuration and patch connectivity affecting species distributions (Damschen et al., 2012)—such as habitat conversion to arable land—and ultimately cascading to the degree of insularity of each edaphic island and associated extinction risk.

Our results seem to challenge some previous views (e.g. Lindborg et al., 2012; Saar et al., 2012) anticipating clonal species to be the obvious winners and non-clonal the losers against local extinction. Here, we revealed that clonal species on edaphic islands display consistent trait responses to variation in insularity and soil conditions, whereas non-clonal plants show distinct and species-specific patterns. This evidence may have far-reaching implications for the conservation biogeography of the studied edaphic island specialists. The consistency of trait patterns may render clonal species more prone to local extinction should insularity or soil conditions vary, for example, due to abrupt changes in the biogeographical setting (e.g. habitat loss) or local environmental factors (e.g. N-deposition). Yet, clonal species may delay their local extinction thanks to their ability to forage, store and share resources amongst interconnected

rooting units forming a clone, potentially allowing them to persist for a long time in remnant populations. Non-clonal plants may instead cope differently with environmental changes because they have a highly species-specific functional spectrum. Depending on the type and severity of the environmental change, some of these species are likely to go locally extinct, whereas others would persist; this, however, may imply some loss of functional diversity. For example, if insularity increases due to habitat loss (resulting in a reduction of island size), *Lychnis* and *Scleranthus* may not be able to cope with this change and not disperse effectively. These species may, therefore, persist only in remnant populations or face local extinction, especially on smaller edaphic islands. Other species, such as *Silene* and *Thymus*—which are weakly or not affected by variation in insularity, soil or microclimate—may instead be used for restoration purposes.

Effective conservation measures should include (1) maintaining large edaphic islands that may contain healthy source populations; (2) identifying and preserving key steppingstones serving as corridors, especially for clonal species and (3) preventing the degradation of edaphic islands (such as habitat loss, conversion or fragmentation), which may reduce the risk of invasion.

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#### CONFLICT OF INTEREST

All authors have no conflicts of interest to declare.

#### DATA AVAILABILITY STATEMENT

The dataset used in this study is available from the Figshare Digital Repository: (<https://doi.org/10.6084/m9.figshare.19698970.v4>) (Ottaviani et al. 2022).

#### PEER REVIEW

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## BIOSKETCH

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Author contributions: G.O. conceived the original research idea; G.O. devised the methodological approach with input from all co-authors; G.O., F.E.M.C. and L.C. collected the field samples; V.J. conducted laboratory analyses; F.E.M.C. measured the insularity metrics; G.O. and F.E.M.C. conducted the statistical analyses; G.O. and J.K. led the writing with input from all co-authors.

## SUPPORTING INFORMATION

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

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