Survival patterns and population stability of cliff plants suggest high resistance to environmental variability

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ABSTRACT

Cliffs are marginal and poorly studied habitats that are home to a high proportion of endemic or threatened species. Here, we review the survival patterns and population dynamics of plants growing on vertical cliffs and compare them to other plants with similar life histories that grow on the ground. To this end, we have compiled studies of cliff and ground plants from two main sources: MONITO and COMPADRE. The resulting data set includes a total of 242 populations of 139 plant species of similar life forms monitored for several years in the northern hemisphere. We tested whether survival rates (Sx), population growth rates, and their temporal variability (lambda: λ±SD) showed similar patterns between cliff and ground plants, and the relationship between them. The review indicates that cliff plants have higher survival rates for both seedlings and older life stages and more stable and less variable population trends over time. Only the survival of post-seedling stages is highly correlated with population dynamics. Altogether, these results suggest that cliff plants may be better equipped to withstand environmental variability than non-specialized plants in more competitive environments.

Keywords

Seedling, Lambda, population trend, matrix model, microsite, temporal fluctuations, climate variability, review, citizen science

INTRODUCTION

The world is currently experiencing the greatest biodiversity crisis ever recorded. This is largely due to significant changes in land cover (Jung et al., 2019; Newbold et al., 2015). Unfortunately, the situation is predicted to worsen due to climate change, as many species are unlikely to be able to adapt to rising temperatures and more frequent heat waves ((Newbold, 2018; Segan et al., 2016). However, as not all species will be affected and respond in the same way to the same stressors, it is not yet clear which habitats, life forms, or traits are more resistant to global change.

Vertical cliffs are likely to have undergone the least change over time due to their limited agricultural and livestock value (Larson et al., 2000). Interestingly, they are also home to many highly specialized rare plants, which are often endemic and threatened according to Red Lists (Datar & Watve, 2018; Fitzsimons & Michael, 2017; Miranda et al., 2022). As a result, these landforms could be considered 'safe habitats' and play an important role from a conservation perspective. However, despite being listed as important habitats (European Commission, 1992), cliffs are poorly studied and the unique biodiversity they harbor is being affected by new human activities, such as the increasing popularity of rock climbing (Lorite et al., 2017; March-Salas et al., 2023).

Despite living in impoverished environments, some cliff plants have been shown to live for hundreds of years, even as herbaceous life forms, and to maintain stable population dynamics ((García, 2003; Larson et al., 2000; picó & Riba, 2002). Both parameters are closely related (García et al., 2008) and seem to be common in marginal or harsh environments such as alpine habitats and cliffs (Forbis & Doak, 2004; Larson et al., 1999; W. F. Morris & Doak, 1998). Long-lived organisms are likely to lie at one of the extremes of the slow-fast continuum (Salguero-Gómez et al., 2016; Walle et al., 2023), representing late reproduction, low reproductive rates, and long lifespans. This would make their long-term persistence less dependent on recruitment than short-lived species (elasticity analysis in matrix population models; Forbis & Doak, 2004; García et al., 2008). This feature is of particular interest in habitats that provide extremely low densities of microsites suitable for seed sowing, germination, or seedling survival. Although low recruitment can be compensated by post-seedling survival (the main vital rate determining population growth rates; (Buckley et al., 2010), achieving minimum recruitment is essential for long-term population and species persistence. Unfortunately, population monitoring often focuses on adult individuals and overlooks the early stages. This hampers our understanding of how recruitment and survival are linked throughout the life cycle of cliff plants, making it difficult to make general statements.

Most cliffs are inaccessible and unaffected by direct human destruction, and life is so difficult that only a limited number of specialized plants can thrive there. Climate change is then the main threat. Climate change is predicted to increase environmental variability in terms of extreme temperatures and intensity of heavy precipitation (IPCC, Seneviratne et al., 2021), which is generally thought to increase the risk of extinction (Boyce, 1992; Menges 1998). This is because climate variability may lead to large shifts in the natural variation of underlying vital rates (birth, growth, survival), which will result in greater temporal variability in population growth rates. However, life history plays a crucial role in the sense that environmental variation can have asymmetric effects on different life stages (Higgins et al., 2000). Understanding how climate variability affects population trends and their temporal variability for each species is critical for setting priorities in conservation planning. And because climate change will affect entire communities, it seems sensible to examine such effects by looking at organisms of similar life forms occurring in similar habitats.

In this study, we searched for studies documenting survival and population growth rates of plants in crevices of vertical cliffs and compared them with those of plants in more classical horizontal soils. We reviewed all available information to identify potential patterns of survival through the life cycle and population dynamics in this challenging environment. Specifically, we tested whether cliff plants have higher survival rates at the seedling stage and later, and more stable population trends (closer to equilibrium and less temporal fluctuation). This information will then be used to discuss their potential vulnerability or resistance in the context of climate warming.

METHODS

Data sources

The MONITO (García et al., 2021) and COMPADRE (Salguero-Gómez et al., 2016) databases were used to obtain information on the survival of seedlings and other life stages, population growth rates, and their temporal variability. Additionally, a few unpublished long-term series were obtained by one of the authors (MBG). We first identified studies that focused on plants growing on vertical cliffs (cliff plants). We then selected studies of plants with similar life forms and macroclimatic conditions that grow on horizontal soil (ground plants). Plants growing on rocky outcrops, screes, or rocky grasslands were excluded due to the high heterogeneity of soil conditions. The geographical distribution of studies included in this review, as well as detailed information used for this study, are shown in Fig. 1 and Appendix A, respectively.

The MONITO database is the result of an ongoing collaborative project, 'Adopt a Plant', which was launched in 2013 in the northeast of the Iberian Peninsula. The project, coordinated by scientists from the Pyrenean Institute of Ecology (CSIC), involves a large number of volunteers and rangers. It covers a broad range of habitats, including Euro-Siberian and Mediterranean, from semi-desert to high alpine. Population trends are estimated through annual monitoring of different plants in fixed plots, which provide time series of population abundance for each species. In cliffs, each plant, including seedlings, is numbered at the time of first observation. This allows relocation in subsequent years and estimation of survival rates of 1-year-old seedlings, 2-year-old seedlings and older plants. The annual survival rate of seedlings (SDL) and older plants (vegetative plus reproductive plants: VR) were estimated separately by calculating the weighted mean of observed individuals within each group over the entire time series. To avoid bias caused by low or sporadic recruitment of cliff plants, we only considered studies in which at least 10 seedlings were recorded over at least three years (Appendix A: Table A.1; "survival dataset"). For comparability with COMPADRE survival rates, which are organized in matrices, we defined seedlings as individuals up to two years old. The procedure for calculating survival rates was consistent across all studies, including unpublished ones conducted by the authors.

García et al. (2021) published MONITO population trends and standard deviations across years. The paper presents population trends in terms of 'population abundance change' (PAch), which is calculated as the geometric mean (λg) of the ratios of population abundance in pairs of consecutive years (λi) and then converted into a percentage using the following formula: $PAch = 100 * (\lambda g - 1)$, where λg is the geometric mean of the annual ratios. For this study, we used λg and the SD of annual ratios (λi) (Appendix A: Table A.2; "trends dataset"). Populations increasing by more than 50% were excluded as they do not represent perennials under natural environmental variability. For comparability with COMPADRE, we excluded populations that did not use censuses for sampling.

On 20 September 2023, we downloaded information from the COMPADRE database, from which studies on cliff plants were initially selected. Since MONITO contributed more to the group of cliff plants (67% of plant species and 65% of populations in the "survival dataset", Appendix A: Table A.1), we selected studies from the COMPADRE database according to specific criteria to assure similar macroclimatic environments to the more central group of cliff plants. Only studies conducted in the northern hemisphere were considered, specifically in tundra (TUN), boreal forest and taiga (BOR), temperate grasslands, savannas and shrublands (TGS), montane grasslands and shrublands (MON), temperate broadleaf and mixed forests (TBM), temperate coniferous forests (TCF), flooded grasslands and savannas (FGS), and Mediterranean forests, woodlands, and scrubs (MED). We excluded trees, shrubs, and annual and succulent plants as they did not have similar life forms as in MONITO. To ensure a fair comparison of survival rates, we excluded studies that involved plant treatments or recent disturbances such as grazing, mowing, or fire. Additionally, we excluded populations whose population trend was greater than 50% to make the dataset comparable to MONITO. Finally, to avoid bias from sampling in a single good or bad year, we only included studies with a time series of at least three years to ensure the reliability of the studies. After selecting the appropriate studies, we extracted two survival rates from each 'survival matrix' corresponding to the combination of year, population, and species: one for the seedling class and the other for the remaining life stages after averaging the survival rates of the different classes. In some studies, the authors did not specify a seedling stage. In these cases, we assumed that the first vegetative class corresponded to the seedling stage. This is a conservative assumption that may have increased the survival rates of seedlings in the COMPADRE dataset compared to the cliff plants provided by the MONITO database.

Population trends in COMPADRE were either provided in the database or calculated as the geometric mean (λg) of lambdas of individual matrices (λi). It is important to note that lambdas in this database are matrix-based and estimated differently than in MONITO, as they represent asymptotic growth rates at a stationary phase after a transitory period. Standard deviations (SD) were calculated from the set of individual lambdas (λi) over the time series for each population.

Conservation status

The conservation status of all species listed in the Red Lists was examined. For European native species, we consulted the European Red List of Threatened Species (UICN, 2023). For North American species, we consulted the NatureServe network (NatureServe, 2023), which uses a classification system similar to the IUCN threat: vulnerable (G3), endangered (G2) and critical (G1). A species was considered threatened if it appeared in any of these catalogues.

Statistical analysis

First, we visually confirmed that the populations of both cliff and ground plants did not differ in the multidimensional environmental space, despite the high concentration of cliff plants in the Iberian Peninsula. To do this, we downloaded four bioclimatic variables from Worldclim (Fick et al., 2017) for the years 1970-2000, with a resolution of 30" longitude/latitude degrees (approximately 1 km). BIO1 (annual mean temperature), BIO5 (maximum temperature of the hottest month), BIO6 (minimum temperature of the coldest month), annual precipitation (BIO12), latitude and altitude data were used to perform a principal component analysis (PCA).

A GLMM was used to compare survival rates, with life stage (SDL and VR) and stratum (rocky in vertical cliffs vs. soil) as fixed factors. Initially, we included two random variables: 'Population' to account for the non-independence of survival rates between SDL and VR plants estimated from the same population, and 'Family' to control for any possible biases on survival rates caused by phylogenetic similarities between species, and the "*lmerTest*" function was applied. Since the model with only the 'Population' random effect resulted in higher R^2 (both marginal and conditional) and lower AIC, we left out the 'Family' random term. The correlation between the survival rates of SDL and VR was also tested with *Pearson's* r for each group of plants.

To assess whether the population trends of both sets of plants deviated similarly from equilibrium (λg = 1) we used populations from the "trends dataset" (Appendix A: Table A.2). We calculated the absolute value of the distance to one and compared the group means of those distances using the Welch test (a non-parametric test was used due to heteroscedasticity). Differences in temporal variation were also examined by comparing the standard deviation between groups using the same test. To assess the possible influence of survival rates of SDLs and VR individuals on population trends and their temporal variation we used a generalized linear model (GLM) with stratum as a fixed factor. For this last test, populations from the "survival dataset" (Appendix A: Table A.1) were coupled with their respective lambdas in the "trends dataset" (Appendix A: Table A.2).

All analyses were performed using R version 4.2.0 (R Core Team, 2022).

RESULTS

The cliff plants were located between 540 - 2337 m a.s.l., while the ground plants covered a slightly larger altitude range: 4-2750 m a.s.l. The exploratory PCA, including 95 populations of 47 plant species, showed that cliff and ground plants did not experience different overall environmental characteristics, despite the high geographical concentration of cliffs (Appendix B). The first PCA axis was associated with BIO1, BIO5, and BIO6 variables. The second PCA axis was mainly associated with altitude and latitude. None of the abiotic variables included in the PCA clustered cliff and ground plant populations, suggesting that potential survival differences were not driven by differences in macroenvironmental parameters.

Plants specialized in vertical cliffs had higher survival rates compared to those that grow on ground sites, both in early (SDL) and later life stages (VR) (Fig. 2 A, Table 1). The variability in survival rates among ground plants was so high that the SDLs of some cliff plants had considerably higher rates than VR individuals of some ground plants. Regardless of the stratum, there was found a positive significant correlation between the survival of SDL and VR, as shown in Fig. 2B (cliffs: r= 0.57, t = 3.37, df = 24, p-value = 0.0025; ground sites: r=0.42, t = 3.74, df = 67, p-value = 0.0004). The GLMM showed significant effects of both stratum ($F_{(1, 93)}$ = 29.557, p-value = 4.352e-07) and life stage ($F_{(1, 94)}$ = 148.236, p-value = 2.2e-16) on survival.

Population trends of cliff plants were significantly closer to equilibrium ($F_{(1, 150.88)}$ = 28.377, p-value = 3.564e-07) and showed significantly lower temporal fluctuations ($F_{(1, 211.58)}$ = 19.001, p-value = 2.038e-05) than ground plants (Fig. 3). Moreover, GLM results showed that, regardless of stratum, the survival rate of VR had a significant effect in reducing both the distance of lambdas to the equilibrium and temporal fluctuations (Table 2 B, D). In the case of survival of SDLs, however, the higher they were the closer to equilibrium were the populations, but the relationship was found to vary between cliffs and ground plants (Table 2 A). Although SDL survival rates tended to reduce population fluctuations, the relationship was not significant (Table 2 C).

DISCUSSION

This study reviewed and compared the survival rates and population dynamics of plants growing on vertical cliffs with those on horizontal ground throughout their life cycle. Although rocky walls limit plant recruitment and growth due to the low density of available microsites and poor nutrient soils, cliff plants exhibit higher survival rates than other plants with similar life forms in less challenging habitats, both at the seedling and older stages. Furthermore, population trends of cliff-dwelling species are closer to equilibrium and have lower temporal variability.

Survival patterns

The few microsites that are suitable for vegetation to grow on vertical cliffs are limited to ledges and crevices. Although humidity may be adequate for seed germination in these areas, the absence of developed soil restricts the ability of seedlings to thrive, making each newly emerged seedling extremely valuable. Our review indicates that survival rates for both seedlings and older plants are higher in the harsh conditions of cliffs, with the former being similar or higher than those of adult plants in some ground sites. Harsh environments may have led to the selection of specific traits that increase survival in hostile conditions worldwide. These traits include water storage in various plant organs to withstand water scarcity (i.e. succulents), and specific traits developed by desiccation-tolerant vascular plants in rock outcrops (Porembski & Barthlott, 2000). The high survival rate of cliff plants may also be attributed to physiological adaptations.

Although our study found a clear pattern of high seedling survival on cliffs, it is important to note that this generalization requires nuance. Firstly, our dataset includes a limited number of populations of cliff plants that belong to just a few taxonomic lineages. Previous studies that examined larger sets of perennial terrestrial plants similar to ours have shown a lack of phylogenetic signal in population dynamics, suggesting that survival rates might be independent between related species (Buckley et al., 2010; García et al., 2021). Secondly, cliffs are highly heterogeneous and offer a variety of microsites that may not be equally suitable for all plants and stages. (Matthes & Larson, 2006) monitored thousands of *Thuja occidentalis* seedlings for 18 years in different microsites and found that 90% of them died a few months after emerging. They found that the safest sites for regeneration were the small features on the vertical cliff face, rather than the large horizontal surfaces, where seedlings had excellent survival rates in crevices despite low emergence. The authors also observed that high maximum summer temperatures reduced survival in horizontal sites, but not in vertical rocky faces.

Since both microsite characteristics and climatic conditions have a joint impact on seedling survival and growth during the early stages of life, it is important to investigate which microsite characteristics can improve survival. Matthes & Larson (2006) proposed that crevices in vertical cliffs provide water-saturated conditions due to hydraulic pressures forcing percolating rainwater into the cracks in the rock. This could facilitate seedlings' access to water while being sheltered from high evaporation by the features in the cliff. In contrast, evaporation would be more pronounced on horizontal or exposed surfaces over shallow soils of rocky outcrops, making horizontal ledges less suitable for plant growth. The importance of rocky microsites for seedling survival extends beyond rocky outcrops and their specialized inhabitants, with studies showing increased seedling success in rocky crevices, caves, or nursery objects in arid ecosystems (Hoffrén & García, 2023).

García et al. (2021) demonstrated that the microtopography of the cliff can also influence the temperature. They placed sensors inside and outside crevices occupied by the endemic cliff plant *Androsace cylindrica* and found that maximum summer temperatures were buffered by several degrees. This effect created a more favorable environment and reduced evaporation during dry periods. Matthes & Larson (2006) found that high maximum temperatures did not increase the hazard for seedlings on the cliff base where *Thuja occidentalis* occurs. It is interesting to note that cliff bases have been proposed as potential microrefugia for contemporary climate change in mountains due to their narrow thermal range on hot days (Hoffrén and García 2023). Thus, crevices and the base of cliffs provide safe sites for specialized plants to grow in, with higher humidity and lower maximum temperature.

Looking forward

Cliff plants are often considered rare worldwide (Fitzsimons & Michael, 2017; Miranda et al., 2022). Our dataset on survival rates shows that most of these plants are endemic, and a significant proportion of them are also threatened (Table 1). This could pose serious problems in the future due to their vulnerability as a result of living in small areas, infrequent habitats, and/or small populations (Harnik et al., 2002). Given that most of this patchy habitat is free from human disturbance, it is worth considering whether cliff plants are more or less likely to persist under current climate change scenarios than those found in more typical conditions.

Contemporary climate change is leading to a rapid redistribution of species' geographic ranges, both in latitude and altitude (Chen et al., 2011). To forecast future distributions in warmer scenarios, species distribution models (SDMs) are frequently employed. However, it may not be appropriate to make broad predictions about the geographic redistribution of species for specialized taxa that rely on microsites. Species with spatially disjunct habitats, such as edaphic endemics (Maclean & Early, 2023), have niches that are defined by factors beyond climate, which are often not considered in SDMs. After incorporating habitat patchiness into distribution models for climate change and reviewing factors and processes that could potentially affect serpentine plant communities in California, (Damschen et al., 2012) concluded that there is no evidence to suggest that plants of rocky habitats are more vulnerable or resistant to climate change than those of 'normal' soil communities. (Csergő et al., 2017) also showed that the performance of one hundred plant species worldwide was not correlated with climate suitability according to macroclimatic models, suggesting that small-scale geographic conditions are the primary drivers of population dynamics. To predict the likelihood of extinction in a warmer and more unpredictable world, it is crucial to understand the life history of the species and identify the demographic mechanisms responsible for population persistence. This can be achieved through population monitoring in naturally fluctuating environments or experimental conditions. (Ehrlén & Morris, 2015) suggest that in order to anticipate the effects of environmental change, it is important to predict local equilibrium across the landscape. Our review analyzed trends and fluctuations of hundreds of populations and found that cliff plants have more stable populations than ground plants.

Variation in population growth rate increases the risk of extinction. However, the impact of variation in underlying vital rates on extinction risk may be more subtle if it affects stages of low impact on the population growth rate. Therefore, the vulnerability of species to increased climatic variability may differ considerably depending on the organism's life history, longevity, and specific survival curve (Halley et al., 2018; W. Morris et al., 2008). Several studies have supported the prediction of life-history theory that vital rates contributing significantly to population growth rate are highly buffered against environmental variability (W. Morris & Doak, 2004). In our study, we observed that the seedling survival rate, which is the most typically variable vital rate, had little or no correlation with population stability. On the contrary, we found that the higher the survival of post-seedling stages, the lower the fluctuations of the population trends. In line with this, (Higgins et al., 2000) decomposed the effect of environmental variance into components that affect recruitment and survival and showed that some populations can benefit from environmental variance if reproductive individuals have high survival rates. This phenomenon, named the 'storage effect', allows populations to be positively influenced by good recruitment years but only marginally influenced by bad years. This could explain why some rare or declining populations may not be at risk due to poor recruitment events, in contrast to populations that recruit on a regular basis (Matthies et al., 2004). Our review suggests that cliff plants are generally stable, but the high seedling survival found may help to boost population growth during occasional recruitment events.

The pattern of higher survival of seedlings and established individuals in cliffs compared to ground plants makes cliff plants less adjusted to the typical “Type III” survival strategy of plants (Harper 1978). Halley et al. (2018) demonstrated that as species move towards the Type III survival strategy, population variability increasingly reflects environmental variation, particularly in earlier life stages, making them more sensitive and vulnerable to climatic variability. In other words, the higher the survival rate of young individuals, the less the environmental variability would affect population trends. The greater survival rate of seedlings on cliffs compared to those on the ground suggests that populations on cliffs may be less vulnerable to climate variability.

CONCLUSION

This study focused on the survival patterns and population dynamics of cliff plants under current natural environmental variability. The deterministic effect of global warming was not investigated, but rather how the observed patterns in cliff plants may make them more or less vulnerable to climatic variability. The review indicates that cliff plants have higher survival rates for both seedlings and older life stages than ground plants, despite the limitations of microsites and nutrients. Additionally, cliff plants exhibit more stable and less variable population trends over time. Altogether, these results suggest that cliff plants may be better equipped to withstand environmental variability than ground plants. We propose that cliffs provide safe sites for specialized plants, reducing their dependence on recruitment and making them less sensitive to environmental fluctuations. These properties should enhance resistance to ongoing climate change and increase the probability of local persistence in the current global change scenario.

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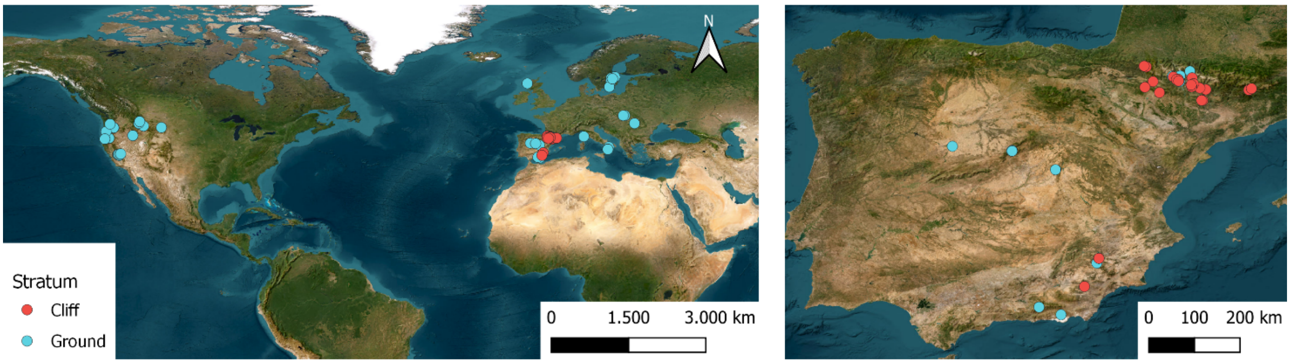

Fig. 1. Geographical distribution of studied populations to compare survival rates of cliff plants (red) vs ground plants (blue) of similar life form in the Northern Hemisphere.

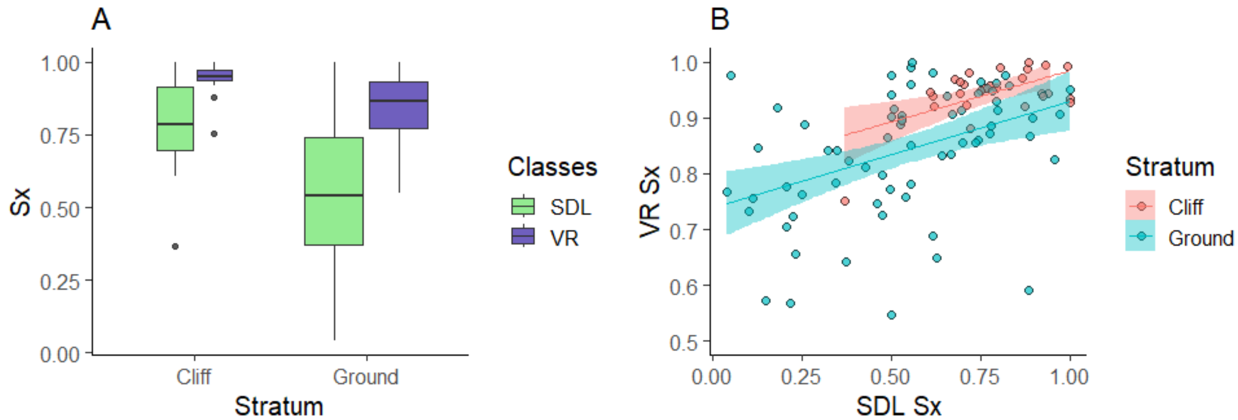

Fig. 2. **(A)** Boxplots of survival rates (Sx) of seedlings (SDL, green) and older stages (VR, purple) of cliffs and ground plants (the width of the boxes reflects the number of populations in each group). **(B)** Pearson's correlation coefficient (±95 CI) between Sx of seedlings and older stages for cliff (red) and ground (blue) plant populations.

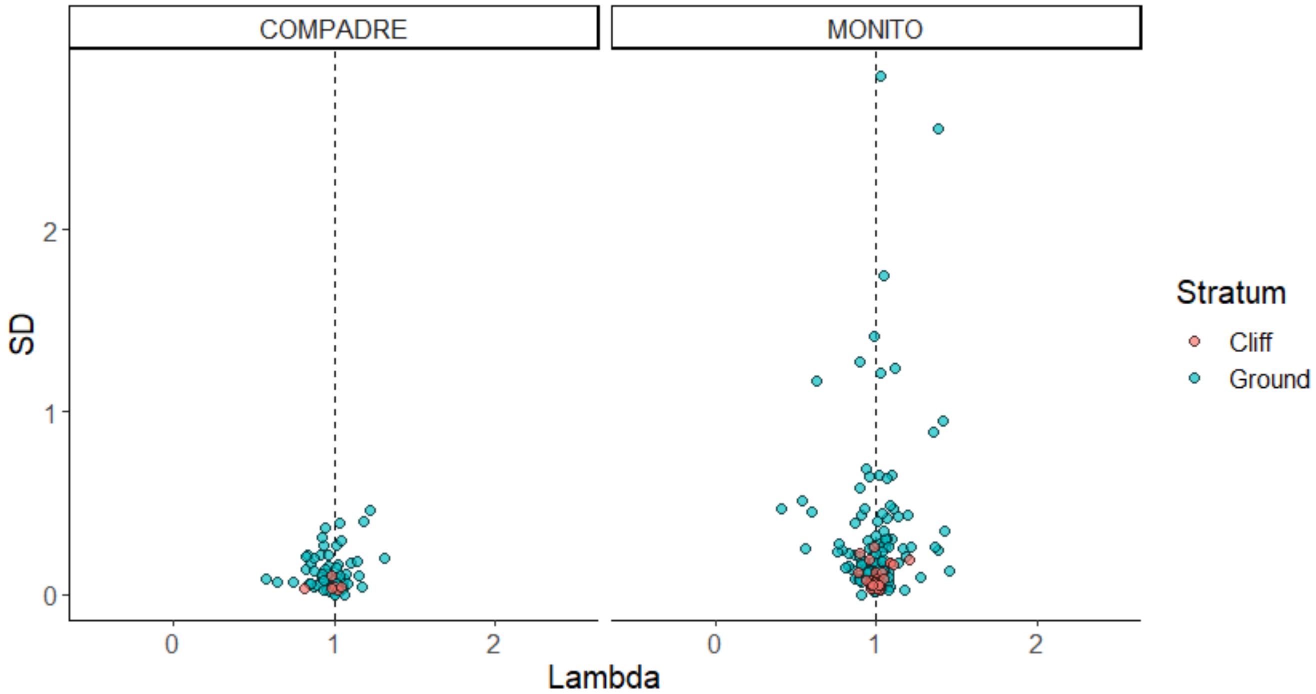

Fig. 3. Relationship between overall population trends and their standard deviation for plants growing on cliffs (red) and horizontal soils (blue). The population of a geophyte (ground plant) was omitted to improve visualization in the MONITO dataset (it did not show up for two consecutive years in a small wetland due to drought; SD = 7.69).

Table 1. Information used to compare cliff and ground plants: number of populations and species (N) for survival rates (Sx) and population dynamics (lambda), percentages of endemic and threatened species; mean ± standard deviation (SD) and range of survival rates for seedlings (SDL) and older stages (VR) in each set of plants.

SURVIVAL RATES	CLIFF PLANTS	GROUND PLANTS
N Species Sx	12	35
N populations Sx	26	69
% Endemic sps	75	40
% Threatened sps	16.67	31.43
Mean Survival SDL	0.79±0.15	0.54±0.24
Range	0.37-1	0.04-1
Mean Survival VR	0.95±0.05	0.84±0.11
Range	0.75-1	0.55-1
POPULATION DYNAMICS	**MONITO**	**COMPADRE**
N species lambda	106	35
N populations lambda	169	71

Table 2. Results of the GLM to test the effect of stratum and survival rates of SDL and VR individuals on the distance of population lambda to equilibrium, and temporal fluctuations of lambda **(A)** and **(C)** SDL, **(B)** and **(C)** VR. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '.

Population trends: distance of lambda to 1.

A

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**	
Intercept	0.46761	0.06669	7.012	4.2E-10	***
VR Sx	-0.46683	0.06922	-6.744	1.44E-09	***
Stratum Ground	0.01443	0.01682	0.858	0.393	

B

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**	
Intercept	0.08668	0.03268	2.653	0.00944	**
SDL Sx	-0.07672	0.03662	-2.095	0.03897	*
Stratum Ground	0.04425	0.02036	2.173	0.03239	*

Population trends: standard deviation of lambdas across years.

C

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**	
Intercept	0.33108	0.08993	3.681	0.000395	***
VR Sx	-0.28389	0.09335	-3.041	0.003087	**
Stratum Ground	0.03109	0.02269	1.371	0.173919	

D

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**	
Intercept	0.10849	0.03824	2.837	0.00562	**
SDL Sx	-0.05817	0.04285	-1.358	0.17799	
Stratum Ground	0.04634	0.02382	1.945	0.05491	.

APPENDIX A

Table A.1. "Survival dataset" including species and population name, source of the data, stratum, seedling's (Sx SDL) and non-seedlings (Sx VR) survival rate, and total number of studied years for each state (seedlings and non-seedlings, N yr SDL and N yr VR respectively).

Species	Populations	Source	Stratum	Sx SDL	Sx VR	N yr SDL	N yr VR
Actaea elata	EUNORR	COMPADRE	Ground	0.700	0.856	4	4
Actaea elata	EUGRASS	COMPADRE	Ground	0.828	0.957	5	5
Actaea elata	WIL032	COMPADRE	Ground	0.742	0.859	6	6
Actaea spicata	Site A	COMPADRE	Ground	0.207	0.778	7	7
Actaea spicata	Site B	COMPADRE	Ground	0.347	0.841	7	7
Agrimonia eupatoria	A	COMPADRE	Ground	0.460	0.747	6	6
Agrimonia eupatoria	B	COMPADRE	Ground	0.793	0.931	6	6
Antirrhinum subbaeticum	Benizar y Hondares	COMPADRE	Cliff	0.676	0.969	6	6
Antirrhinum subbaeticum	Bogarra, Potiche y Mundo	COMPADRE	Cliff	0.921	0.943	6	6
Armeria caespitosa	Loma de Cabezas	COMPADRE	Ground	0.553	0.782	4	4
Armeria caespitosa	Peñalara Peak	COMPADRE	Ground	0.489	0.865	4	4
Astragalus tremolsianus	Sierra de Grador	COMPADRE	Ground	0.555	0.959	6	6
Astragalus tyghensis	Site 4	COMPADRE	Ground	0.474	0.798	10	10
Astragalus tyghensis	Site 10	COMPADRE	Ground	0.323	0.840	10	10
Astragalus tyghensis	Site 25	COMPADRE	Ground	0.378	0.823	10	10
Astragalus tyghensis	Site 41	COMPADRE	Ground	0.426	0.812	10	10
Astragalus tyghensis	Site 13	COMPADRE	Ground	0.342	0.784	10	10
Balsamorhiza sagittata	Mount Jumbo	COMPADRE	Ground	0.769	0.952	6	6
Boechera fecunda	Vipond park	COMPADRE	Ground	0.625	0.648	5	5
Boechera fecunda	Charleys Gulch	COMPADRE	Ground	0.497	0.772	7	7
Brassica insularis	Teghime	COMPADRE	Ground	0.694	0.914	10	10
Corallorhiza trifida	Ordesa	COMPADRE	Ground	0.885	0.592	6	6
Cypripedium calceolus	Pineta	COMPADRE	Ground	0.780	0.886	3	3
Cypripedium calceolus	Sallent	COMPADRE	Ground	0.670	0.905	5	5
Cypripedium fasciculatum	Region 3	COMPADRE	Ground	0.748	0.947	8	8
Cypripedium fasciculatum	Region 5	COMPADRE	Ground	0.783	0.949	8	8
Dorycnium spectabile	Barranco del Agua	COMPADRE	Ground	0.554	0.851	6	6
Dracocephalum austriacum	Zadielsky kamen (S1)	COMPADRE	Ground	0.818	0.976	4	4
Dracocephalum austriacum	Zelezne vrata (S3)	COMPADRE	Ground	0.554	0.989	4	4
Helianthemum polygonoides	Cordovilla	COMPADRE	Ground	0.640	0.833	6	6
Laserpitium longiradium	Sierra Nevada	COMPADRE	Ground	0.750	0.964	6	6
Lathyrus vernus	L	COMPADRE	Ground	0.655	0.938	4	4
Lathyrus vernus	T4	COMPADRE	Ground	0.793	0.963	4	4
Lepidium davisii	Playa A-1	COMPADRE	Ground	0.500	0.902	3	3
Lepidium davisii	Playa A-2	COMPADRE	Ground	0.500	0.942	3	3
Lepidium davisii	Playa A-3	COMPADRE	Ground	0.050	0.975	3	3
Lepidium davisii	Playa A-5	COMPADRE	Ground	0.250	0.763	3	3
Lepidium davisii	Playa A-6	COMPADRE	Ground	0.125	0.847	3	3
Lepidium davisii	Playa C-10	COMPADRE	Ground	0.500	0.976	3	3
Limonium erectum	Pangia	COMPADRE	Ground	0.735	0.856	6	6
Limonium malacitanum	El Chantal (El Cantal)	COMPADRE	Cliff	0.368	0.751	6	6

Lomatium bradshawii	LongTom	COMPADRE	Ground	0.473	0.725	8	8
Lomatium cookii	Middle	COMPADRE	Ground	0.775	0.871	6	6
Lomatium cookii	South	COMPADRE	Ground	0.616	0.688	6	6
Lupinus lepidus	SERE 3, Lower	COMPADRE	Ground	0.501	0.547	5	5
Mimulus cardinalis	Buck Meadows	COMPADRE	Ground	0.148	0.574	4	4
Mimulus cardinalis	Rainbow	COMPADRE	Ground	0.218	0.568	4	4
Mimulus cardinalis	Wawona	COMPADRE	Ground	0.207	0.704	4	4
Mimulus cardinalis	Carlon	COMPADRE	Ground	0.111	0.757	4	4
Mimulus lewisii	Wawona	COMPADRE	Ground	0.100	0.732	4	4
Mimulus lewisii	Carlon	COMPADRE	Ground	0.231	0.657	4	4
Mimulus lewisii	May Lake	COMPADRE	Ground	0.180	0.917	4	4
Mimulus lewisii	Warren Fork	COMPADRE	Ground	0.258	0.888	4	4
Plantago coronopus	ES	COMPADRE	Ground	0.223	0.724	4	4
Potentilla anserina	Near Stockholm	COMPADRE	Ground	0.040	0.768	4	4
Primula farinosa	Karbomosse	COMPADRE	Ground	0.971	0.907	4	4
Primula farinosa	Flottskär	COMPADRE	Ground	0.741	0.942	4	4
Primula farinosa	Rossholm	COMPADRE	Ground	0.507	0.915	4	4
Psoralea esculenta	Montana Crow Indian Reservation	COMPADRE	Ground	0.556	1.000	4	4
Ramonda myconi	Ingla1	COMPADRE	Cliff	0.608	0.946	6	6
Ramonda myconi	Ingla2	COMPADRE	Cliff	0.718	0.981	5	5
Ramonda myconi	Urus	COMPADRE	Cliff	0.884	1.000	4	4
Saponaria bellidifolia	Dealul Vidolm	COMPADRE	Ground	1.000	0.950	4	4
Serapias cordigera	Cerchiara	COMPADRE	Ground	0.893	0.898	6	6
Serapias cordigera	Falconara Albanese	COMPADRE	Ground	0.956	0.826	6	6
Serapias cordigera	San Biase	COMPADRE	Ground	0.886	0.868	9	9
Silene ciliata	Dos Hermanas	COMPADRE	Ground	0.614	0.981	4	4
Silene ciliata	Laguna	COMPADRE	Ground	0.666	0.834	4	4
Succisa pratensis	Roadverge	COMPADRE	Ground	0.538	0.757	4	4
Succisa pratensis	Moist ungrazed	COMPADRE	Ground	0.372	0.641	4	4
Trillium ovatum	Big Creek, Bitterroot Valley	COMPADRE	Ground	0.530	0.898	5	5
Trillium ovatum	Grant Creek, Missoula Valley	COMPADRE	Ground	0.530	0.903	5	5
Trillium ovatum	Spring Gulch, Rattlesnake drainage	COMPADRE	Ground	0.530	0.895	5	5
Androsace cylindrica	andcyc_carq	MONITO	Cliff	0.872	0.919	6	7
Androsace cylindrica	andcyh_ache	MONITO	Cliff	0.775	0.956	7	10
Androsace cylindrica	andcyh_linz	MONITO	Cliff	0.938	0.944	3	11
Androsace cylindrica	andcyw_oroe	MONITO	Cliff	0.991	0.993	8	10
Androsace pyrenaica	andpyr_barb	MONITO	Cliff	0.865	0.971	4	7
Androsace pyrenaica	andpyr_ses1	MONITO	Cliff	1.000	0.934	3	6
Androsace pyrenaica	andpyr_ses2	MONITO	Cliff	1.000	0.926	3	9
Petrocoptis crassifolia	petcra_serc	MONITO	Cliff	0.614	0.939	11	13
Petrocoptis montsicciana	petmon_bera	MONITO	Cliff	0.702	0.960	8	9
Petrocoptis montsicciana	petmon_mont	MONITO	Cliff	0.792	0.953	6	10
Petrocoptis montsicciana	petmon_salt	MONITO	Cliff	0.711	0.921	9	10
Petrocoptis pseudoviscosa	petpse_abi	MONITO	Cliff	0.760	0.954	5	6
Petrocoptis pseudoviscosa	Fchurro	MONITO	Cliff	0.691	0.964	5	6
Petrocoptis pseudoviscosa	petpse_argo	MONITO	Cliff	0.924	0.939	4	7
Polygonum viviparum	polviv_prad	MONITO	Ground	0.797	0.914	3	4
Sarcocapnos enneaphylla	roqueB_añis	MONITO	Cliff	0.719	0.880	5	7

Saxifraga longifolia	saxlon_pant	MONITO	Cliff	0.693	0.943	5	6
Thymus vulgaris	thyvul_añis	MONITO	Ground	0.526	0.887	3	4
Valeriana longiflora	vallon_rold	MONITO	Cliff	0.617	0.920	9	11
Borderea chouardii	barranco	Unpublished	Cliff	0.803	0.990	19	22
Borderea chouardii	cantera	Unpublished	Cliff	0.880	0.987	10	11
Borderea chouardii	cueva	Unpublished	Cliff	0.931	0.995	7	8

Table A.2. "Trends dataset" including species and population name, source of the data, stratum, lambda (λ) and it's standard deviation (λ sd), and the total number of studied years for each population (N yr).

Species	**Populations**	**Source**	**Stratum**	**λ**	**λ sd**	**N yr**
Actaea elata	EUNORR	COMPADRE	Ground	1.15	0.10	4
Actaea elata	EUGRASS	COMPADRE	Ground	0.94	0.36	5
Actaea elata	WIL033	COMPADRE	Ground	0.98	0.08	6
Actaea spicata	Site A	COMPADRE	Ground	0.97	0.11	7
Actaea spicata	Site B	COMPADRE	Ground	0.95	0.11	7
Agrimonia eupatoria	A	COMPADRE	Ground	0.97	0.04	6
Agrimonia eupatoria	B	COMPADRE	Ground	1.04	0.08	6
Antirrhinum subbaeticum	Benizar y Hondares	COMPADRE	Cliff	1.00	0.04	6
Antirrhinum subbaeticum	Bogarra, Potiche y Mundo	COMPADRE	Cliff	1.03	0.02	6
Armeria caespitosa	Loma de Cabezas	COMPADRE	Ground	1.03	0.09	4
Armeria caespitosa	Peñalara Peak	COMPADRE	Ground	1.05	0.03	4
Astragalus tremolsianus	Sierra de Grador	COMPADRE	Ground	1.01	0.06	6
Astragalus tyghensis	Site 4	COMPADRE	Ground	0.91	0.22	10
Astragalus tyghensis	Site 10	COMPADRE	Ground	1.03	0.17	10
Astragalus tyghensis	Site 25	COMPADRE	Ground	1.03	0.39	10
Astragalus tyghensis	Site 41	COMPADRE	Ground	0.94	0.27	10
Astragalus tyghensis	Site 13	COMPADRE	Ground	1.04	0.30	10
Balsamorhiza sagittata	Mount Jumbo	COMPADRE	Ground	0.94	0.08	6
Boechera fecunda	Charleys Gulch	COMPADRE	Ground	0.97	0.15	7
Boechera fecunda	Vipond park	COMPADRE	Ground	1.22	0.47	5
Brassica insularis	Teghime	COMPADRE	Ground	1.01	0.15	10
Corallorhiza trifida	Ordesa	COMPADRE	Ground	0.89	0.05	6
Cypripedium calceolus	Pineta	COMPADRE	Ground	1.02	0.05	3
Cypripedium calceolus	Sallent	COMPADRE	Ground	1.03	0.10	5
Cypripedium fasciculatum	Region 3	COMPADRE	Ground	1.00	0.07	8
Cypripedium fasciculatum	Region 5	COMPADRE	Ground	1.02	0.06	8
Dorycnium spectabile	Barranco del Agua	COMPADRE	Ground	1.18	0.40	6
Dracocephalum austriacum	Zadielsky kamen (S1)	COMPADRE	Ground	1.08	0.06	4
Dracocephalum austriacum	Zelezne vrata (S3)	COMPADRE	Ground	1.07	0.00	4
Helianthemum polygonoides	Cordovilla	COMPADRE	Ground	0.95	0.11	6
Laserpitium longiradium	Sierra Nevada	COMPADRE	Ground	0.93	0.08	6
Lathyrus vernus	L	COMPADRE	Ground	1.05	0.05	4
Lathyrus vernus	T1	COMPADRE	Ground	0.97	0.06	4

Lepidium davisii	Playa A-1	COMPADRE	Ground	0.96	0.02	3
Lepidium davisii	Playa A-2	COMPADRE	Ground	0.92	0.10	3
Lepidium davisii	Playa A-3	COMPADRE	Ground	0.93	0.11	3
Lepidium davisii	Playa A-5	COMPADRE	Ground	0.88	0.13	3
Lepidium davisii	Playa A-6	COMPADRE	Ground	0.82	0.21	3
Lepidium davisii	Playa C-10	COMPADRE	Ground	0.98	0.02	3
Limonium erectum	Pangia	COMPADRE	Ground	0.94	0.14	6
Limonium malacitanum	El Chantal (El Cantal)	COMPADRE	Cliff	0.81	0.03	6
Lomatium bradshawii	LongTom	COMPADRE	Ground	0.83	0.22	8
Lomatium cookii	Middle	COMPADRE	Ground	1.10	0.17	6
Lomatium cookii	South	COMPADRE	Ground	0.92	0.31	6
Lupinus lepidus	SERE 3, Lower	COMPADRE	Ground	1.31	0.20	5
Mimulus cardinalis	Buck Meadows	COMPADRE	Ground	0.65	0.07	4
Mimulus cardinalis	Rainbow	COMPADRE	Ground	0.58	0.08	4
Mimulus cardinalis	Wawona	COMPADRE	Ground	1.01	0.27	4
Mimulus cardinalis	Carlon	COMPADRE	Ground	1.17	0.04	4
Mimulus lewisii	Wawona	COMPADRE	Ground	0.83	0.14	4
Mimulus lewisii	Carlon	COMPADRE	Ground	0.86	0.17	4
Mimulus lewisii	May Lake	COMPADRE	Ground	1.01	0.05	4
Mimulus lewisii	Warren Fork	COMPADRE	Ground	1.14	0.18	4
Plantago coronopus	ES	COMPADRE	Ground	0.97	0.22	4
Potentilla anserina	Near Stockholm	COMPADRE	Ground	0.88	0.20	4
Primula farinosa	Karbomosse	COMPADRE	Ground	1.06	0.08	4
Primula farinosa	Flottskär	COMPADRE	Ground	1.07	0.11	4
Primula farinosa	Rossholm	COMPADRE	Ground	0.97	0.03	4
Psoralea esculenta	Montana Crow Indian Reservation	COMPADRE	Ground	1.02	0.03	4
Ramonda myconi	Ingla1	COMPADRE	Cliff	0.98	0.11	6
Ramonda myconi	Ingla2	COMPADRE	Cliff	0.98	0.03	5
Ramonda myconi	Urus	COMPADRE	Cliff	1.04	0.04	4
Saponaria bellidifolia	Dealul Vidolm	COMPADRE	Ground	0.97	0.04	4
Serapias cordigera	Cerchiara	COMPADRE	Ground	0.88	0.04	6
Serapias cordigera	Falconara Albanese	COMPADRE	Ground	0.85	0.06	6
Serapias cordigera	San Biase	COMPADRE	Ground	0.86	0.06	9
Succisa pratensis	Roadverge	COMPADRE	Ground	0.93	0.02	4
Succisa pratensis	Moist ungrazed	COMPADRE	Ground	0.74	0.07	4
Trillium ovatum	Big Creek, Bitterroot Valley	COMPADRE	Ground	1.04	0.02	5
Trillium ovatum	Grant Creek, Missoula Valley	COMPADRE	Ground	1.00	0.00	5
Trillium ovatum	Spring Gulch, Rattlesnake drainage	COMPADRE	Ground	1.00	0.00	5
Actaea spicata	actspi_monc	MONITO	Ground	0.91	0.44	10
Allium ursinum ursinum	allurs_monc	MONITO	Ground	0.89	0.59	10
Androsace cylindrica cylindrica	andcyc_carq	MONITO	Cliff	1.00	0.07	10
Androsace cylindrica cylindrica	andcyc_cer1	MONITO	Cliff	0.97	0.08	3
Androsace cylindrica hirtella	andcyh_ache	MONITO	Cliff	0.97	0.07	6
Androsace cylindrica hirtella	andcyh_linz	MONITO	Cliff	0.99	0.12	6
Androsace cylindrica willkommii	andcyw_oroe	MONITO	Cliff	0.98	0.05	6
Androsace pyrenaica	andpyr_barb	MONITO	Cliff	0.96	0.06	5
Androsace pyrenaica	andpyr_chis	MONITO	Cliff	0.98	0.03	3
Androsace pyrenaica	andpyr_coma	MONITO	Cliff	0.98	0.03	5

Androsace pyrenaica	andpyr_ses1	MONITO	Cliff	0.98	0.26	6
Androsace pyrenaica	andpyr_ses2	MONITO	Cliff	0.97	0.03	5
Androsace vitaliana assoana	andvit_java	MONITO	Ground	1.06	0.04	3
Arenaria tetraquetra tetraquetra	aretet_guar	MONITO	Ground	0.97	0.17	8
Arnica montana montana	arnmon_astu	MONITO	Ground	0.98	0.13	6
Arnica montana montana	arnmon_form	MONITO	Ground	1.00	0.05	6
Arnica montana montana	arnmon_paqu	MONITO	Ground	1.03	0.18	6
Arnica montana montana	arnmon_vall	MONITO	Ground	1.03	0.18	5
Artemisia eriantha	arteri_fuls	MONITO	Ground	0.98	0.26	5
Artemisia eriantha	arteri_infi	MONITO	Ground	0.98	0.12	5
Asphodelus fistulosus	nardub_alfo	MONITO	Ground	0.77	0.28	4
Asphodelus fistulosus	narpal_monc	MONITO	Ground	1.03	0.10	5
Astragalus clusianus	astclu_gall	MONITO	Ground	0.99	0.05	3
Astragalus exscapus	astexs_almu	MONITO	Ground	1.03	0.05	3
Borderea chouardii	borcho_sope	MONITO	Cliff	1.02	0.03	5
Borderea pyrenaica	borpyr_cust	MONITO	Ground	0.95	0.13	10
Borderea pyrenaica	borpyr_cuta	MONITO	Ground	1.06	0.13	4
Botrychium lunaria	botlun_sanj	MONITO	Ground	0.89	0.09	4
Calamintha grandiflora	calgra_buja	MONITO	Ground	1.01	0.16	10
Carduus carlinoides carlinoides	vicarg_mond	MONITO	Ground	1.03	0.18	5
Carex bicolor	humeda_carr	MONITO	Ground	0.93	0.18	7
Carex bicolor	humeda_luen	MONITO	Ground	1.04	0.26	7
Centaurea pinnata	cenpin_codo	MONITO	Ground	1.10	0.65	6
Centaurea pinnata	cenpin_enci	MONITO	Ground	0.85	0.14	5
Centaurea pinnata	cenpin_nomb	MONITO	Ground	1.05	1.75	5
Cheilanthes acrostica	notmar_esto	MONITO	Ground	1.06	0.64	5
Cistus clusii clusii	cisclu_colu	MONITO	Ground	0.95	0.09	5
Colchicum triphyllum	stecol_leci	MONITO	Ground	0.90	0.08	4
Coronopus navasii	cornav_used	MONITO	Ground	0.99	0.23	4
Cypripedium calceolus	cypcal_cota	MONITO	Ground	0.87	0.21	4
Cypripedium calceolus	cypcal_sal1	MONITO	Ground	1.02	0.02	3
Cypripedium calceolus	cypcal_sal2	MONITO	Ground	0.96	0.14	3
Dactylorhiza maculata	humeda_lumi	MONITO	Ground	0.75	0.23	3
Drosera rotundifolia	drorot_monc	MONITO	Ground	0.63	1.17	10
Erinacea anthyllis	lomgra_exea	MONITO	Ground	1.16	0.25	4
Erodium glandulosum	erogla_port	MONITO	Ground	1.06	0.26	4
Erodium paularense	eropau_orca	MONITO	Ground	1.03	0.07	5
Erodium paularense	eropau_pico	MONITO	Ground	1.01	0.04	5
Euphorbia nevadensis ssp.	eupnev_lues	MONITO	Ground	0.91	0.17	5
Euphorbia nevadensis ssp.	eupnev_monc	MONITO	Ground	0.95	0.30	5
Euphorbia nevadensis ssp.	eupnev_oroe	MONITO	Ground	1.07	0.16	5
Ferula loscosii	ferlos_almu	MONITO	Ground	0.95	0.16	3
Ferula loscosii	ferlos_chip	MONITO	Ground	1.04	0.28	8
Ferula loscosii	ferlos_faba	MONITO	Ground	0.91	0.00	3
Galanthus nivalis	galniv_aisa	MONITO	Ground	0.90	0.10	5
Galanthus nivalis	galniv_añis	MONITO	Ground	1.03	0.05	5
Galanthus nivalis	galniv_cedr	MONITO	Ground	0.99	0.13	4
Galanthus nivalis	galniv_gavi	MONITO	Ground	0.87	0.08	5

Galanthus nivalis	galniv_sanj	MONITO	Ground	0.89	0.09	5
Genista scorpius	astclu_gall	MONITO	Ground	0.96	0.08	3
Genista scorpius	cenpin_nomb	MONITO	Ground	0.95	0.11	5
Gentiana lutea lutea	genlut_blan	MONITO	Ground	1.05	0.11	6
Gentiana lutea lutea	genlut_esto	MONITO	Ground	1.01	0.65	5
Gentiana lutea lutea	genlut_otur	MONITO	Ground	0.96	0.11	4
Gentiana lutea lutea	genlut_zuri	MONITO	Ground	1.00	0.28	6
Goodyera repens	goorep_paco	MONITO	Ground	0.60	0.45	5
Goodyera repens	goorep_sabi	MONITO	Ground	0.79	0.24	4
Helianthemum squamatum	yesera_barb	MONITO	Ground	1.41	0.95	3
Helianthemum squamatum	yesera_cuar	MONITO	Ground	1.00	0.22	3
Helianthemum syriacum	yesera_barb	MONITO	Ground	1.35	0.89	3
Herniaria fruticosa	yesera_barb	MONITO	Ground	1.02	2.84	3
Herniaria fruticosa	yesera_vill	MONITO	Ground	0.94	0.12	3
Horminum pyrenaicum	horpyr_lech	MONITO	Ground	1.01	0.16	6
Huperzia selago	hupsel_aigu	MONITO	Ground	0.99	0.18	3
Huperzia selago	hupsel_bach	MONITO	Ground	0.98	0.12	6
Huperzia selago	hupsel_mill	MONITO	Ground	0.99	0.32	5
Hypericum caprifolium	tobera_alia	MONITO	Ground	1.20	0.43	4
Inula crithmoides	salada_zuer	MONITO	Ground	0.91	0.06	3
Iris graminea	irigra_boal	MONITO	Ground	1.08	0.04	5
Iris latifolia	thytin_cuta	MONITO	Ground	1.12	1.24	3
Jurinea pinnata	jurpin_cala	MONITO	Ground	1.10	0.30	8
Jurinea pinnata	yesera_vill	MONITO	Ground	1.03	0.13	3
Krascheninnikovia ceratoides	kracer_pin1	MONITO	Ground	0.99	0.01	4
Lathyrus vernus vernus	latver_biel	MONITO	Ground	0.91	0.18	10
Lavandula stoechas pedunculata	lavsto_alpa	MONITO	Ground	1.03	0.04	5
Lepidium subulatum	yesera_cuar	MONITO	Ground	0.96	0.13	3
Limonium latebracteatum	limste_chip	MONITO	Ground	0.94	0.15	5
Limonium stenophyllum	limste_chip	MONITO	Ground	0.90	0.21	5
Limonium stenophyllum	salada_rebo	MONITO	Ground	1.08	0.02	3
Lithodora fruticosa	yesera_barb	MONITO	Ground	1.14	0.17	3
Lomelosia graminifolia graminifolia	lomgra_exea	MONITO	Ground	1.00	0.02	4
Merendera montana	mermon_guas	MONITO	Ground	1.06	0.31	3
Narcissus albicans	naralb_alpa	MONITO	Ground	1.38	2.55	5
Narcissus asturiensis jacetanus	narjac_aisa	MONITO	Ground	1.05	0.31	4
Narcissus asturiensis jacetanus	narjac_anso	MONITO	Ground	1.04	0.16	5
Narcissus asturiensis jacetanus	narjac_liza	MONITO	Ground	1.08	0.07	5
Narcissus asturiensis jacetanus	narjac_lues	MONITO	Ground	0.95	0.11	5
Narcissus bulbocodium bulbocodium	narbul_bron	MONITO	Ground	0.91	0.16	3
Narcissus bulbocodium bulbocodium	narbul_holl	MONITO	Ground	0.93	0.47	5
Narcissus bulbocodium bulbocodium	narbul_luci	MONITO	Ground	1.03	1.21	5
Narcissus dubius	nardub_alfo	MONITO	Ground	0.83	0.16	4
Narcissus pallidulus	narpal_alpa	MONITO	Ground	0.99	1.41	5
Narcissus pallidulus	narpal_ligr	MONITO	Ground	1.04	0.19	4
Narcissus pallidulus	narpal_monc	MONITO	Ground	1.22	0.26	5
Narcissus rupicola	narrup_used	MONITO	Ground	1.07	0.41	5
Notholaena marantae	notmar_esto	MONITO	Ground	1.09	0.49	5

Ophioglossum vulgatum	ophvul_guar	MONITO	Ground	0.96	7.69	8
Ophioglossum vulgatum	ophvul_royu	MONITO	Ground	1.14	0.43	3
Ophrys ciliata	ophcil_torr	MONITO	Ground	0.55	0.25	5
Orchis anthropophora	orcant_tala	MONITO	Ground	1.45	0.13	3
Orthilia secunda	goorep_paco	MONITO	Ground	0.41	0.47	4
Orthilia secunda	goorep_sabi	MONITO	Ground	0.54	0.51	3
Paeonia officinalis microcarpa	paeoff_baño	MONITO	Ground	1.27	0.09	3
Papaver lapeyrousianum	paplap_ball	MONITO	Ground	0.81	0.15	3
Paris quadrifolia	actspi_monc	MONITO	Ground	1.01	0.40	10
Petrocoptis crassifolia	petcra_serc	MONITO	Cliff	1.00	0.08	9
Petrocoptis crassifolia	roqueB_añis	MONITO	Cliff	1.05	0.08	3
Petrocoptis guarensis	roqueB_alqu	MONITO	Cliff	1.11	0.16	3
Petrocoptis hispanica	pethis_sanj	MONITO	Cliff	1.00	0.05	6
Petrocoptis montsicciana	petmon_bera	MONITO	Cliff	0.96	0.05	5
Petrocoptis montsicciana	petmon_chir	MONITO	Cliff	1.04	0.12	6
Petrocoptis montsicciana	petmon_mont	MONITO	Cliff	0.98	0.06	6
Petrocoptis montsicciana	petmon_salt	MONITO	Cliff	0.98	0.06	6
Petrocoptis pseudoviscosa	petpse_abi	MONITO	Cliff	1.03	0.03	5
Petrocoptis pseudoviscosa	petpse_argo	MONITO	Cliff	1.00	0.07	5
Petrocoptis pseudoviscosa	petpse_vent	MONITO	Cliff	1.01	0.03	5
Pinguicula alpina	pinalp_orde	MONITO	Cliff	1.09	0.17	7
Pinguicula grandiflora grandiflora	tobera_sarr	MONITO	Ground	1.04	0.23	4
Pinguicula longifolia longifolia	pinlon_buj1	MONITO	Cliff	1.09	0.18	9
Pinguicula vulgaris	spiaes_grie	MONITO	Ground	0.95	0.11	3
Pinguicula vulgaris	spiaes_guad	MONITO	Ground	0.95	0.25	6
Plantago albicans	yesera_barb	MONITO	Ground	1.37	0.26	3
Plantago lanceolata	plalan_pant	MONITO	Ground	1.04	0.08	4
Plantago monosperma monosperma	thytin_cuta	MONITO	Ground	1.08	0.26	3
Polygonum viviparum	polviv_prad	MONITO	Ground	1.38	0.24	4
Primula farinosa	tobera_sarr	MONITO	Ground	1.07	0.09	4
Primula integrifolia	saxcot_pant	MONITO	Ground	1.01	0.09	3
Pyrola minor	pyrmin_arag	MONITO	Ground	1.05	0.08	3
Ramonda myconi	andpyr_ses1	MONITO	Cliff	1.02	0.05	6
Ramonda myconi	rammyc_añis2	MONITO	Cliff	0.89	0.12	3
Ramonda myconi	rammyc_rold	MONITO	Cliff	1.01	0.03	8
nunculus parnassiifolius heterocarp	borpyr_cust	MONITO	Ground	0.98	0.09	6
Rosmarinus officinalis	cisclu_colu	MONITO	Ground	0.95	0.09	5
Sarcocapnos enneaphylla	roqueB_alqu	MONITO	Cliff	1.21	0.19	3
Sarcocapnos enneaphylla	roqueB_añis	MONITO	Cliff	1.01	0.06	3
Saxifraga corsica cossoniana	saxcor_manz	MONITO	Ground	1.43	0.35	3
Saxifraga cotyledon	saxcot_frai	MONITO	Cliff	0.96	0.05	6
Saxifraga cotyledon	saxcot_pant	MONITO	Cliff	1.02	0.05	3
Saxifraga hariotii	saxhar_bisa	MONITO	Ground	0.98	0.05	6
Saxifraga longifolia	saxlon_blan	MONITO	Cliff	0.94	0.08	6
Saxifraga longifolia	saxlon_pant	MONITO	Cliff	1.01	0.05	6
Saxifraga moncayensis	saxmon_monc	MONITO	Cliff	0.95	0.19	10
Scrophularia alpestris	scralp_monc	MONITO	Ground	0.87	0.39	10
Silene acaulis	silaca_capr	MONITO	Ground	0.94	0.08	7

Spiranthes aestivalis	spiaes_grie	MONITO	Ground	0.93	0.69	3
Spiranthes aestivalis	spiaes_guad	MONITO	Ground	1.05	0.35	6
Spiranthes aestivalis	spiaes_orih	MONITO	Ground	0.96	0.65	4
Spiranthes spiralis	spispi_monz	MONITO	Ground	1.19	0.21	4
Sternbergia colchiciflora	stecol_leci	MONITO	Ground	0.90	1.27	4
Thapsia villosa	lavsto_alpa	MONITO	Ground	1.10	0.47	5
Thymelaea subrepens	thysub_mosc	MONITO	Ground	1.04	0.45	3
Thymus vulgaris ssp.	erogla_port	MONITO	Ground	1.08	0.12	4
Thymus vulgaris ssp.	thyvul_añis	MONITO	Ground	0.94	0.09	4
Thymus zygis ssp.	eropau_orca	MONITO	Ground	0.83	0.22	5
Thymus zygis ssp.	eropau_pico	MONITO	Ground	1.03	0.07	5
Valeriana longiflora	pethis_sanj	MONITO	Cliff	0.90	0.22	6
Valeriana longiflora	vallon_rold	MONITO	Ground	1.04	0.13	10
Vella pseudocytisus paui	velpse_vill	MONITO	Ground	1.17	0.02	3
Woodsia alpina	wooalp_espe	MONITO	Cliff	0.97	0.05	6

APPENDIX B

Multidimensional location of the populations studied and each variable in a Principal Component Analysis (PCA). The mean for each group of plants (cliffs and ground; Ellipse level= 0.95) is depicted by empty symbols. Cliffs: red dots. Ground: blue dots. Variables: BIO1 (Annual Mean Temperature), BIO5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month), BIO12 (Annual Precipitation).