Received: 11 February 2021 | Revised: 27 July 2021 | Accepted: 29 July 2021

DOI: 10.1111/avsc.12614

Applied Vegetation Science IAVS

RESEARCH ARTICLE

Sentinel 2 images enable reliable prediction of fine-scale habitat dynamics of narrow endemic plant species in serpentine soils

Sara Ponce-Fontenla[1] | Miguel Serrano[2] | Roi Carballal[2] | Adrián Regos[1,3]

[1]Departamento de Zooloxía, Xenética e Antropoloxía Física, Universidade de Santiago de Compostela, Santiago de Compostela, Spain

[2]Departamento de Botánica, Universidade de Santiago de Compostela, Santiago de Compostela, Spain

[3]InBIO/CIBIO – Centro de Investigação em Biodiversidade e Recursos Genéticos, Vairão, Portugal

Correspondence
Adrián Regos, Departamento de Zooloxía, Xenética e Antropoloxía Física, Universidade de Santiago de Compostela, 15782 Santiago de Compostela, Spain.
Email: adrian.regos@usc.es

Funding information
MS, RC and AR received financial support from the Xunta de Galicia (ED431B 2018/36). AR was funded by the Xunta de Galicia (ED481B2016/084-0)

Co-ordinating Editor: Hannes Feilhauer

Abstract

Aims: Serpentine soils are rare globally, covering <1% of the land surface, but frequently harbouring large numbers of narrow endemic species. Many serpentine areas are endangered and would benefit from actions informed by species distribution models (SDMs). Here, we assessed, for the first time, the potential use of remotely sensed descriptors of water and carbon cycles derived from Copernicus Sentinel 2 images for fine-scale habitat characterization and mapping of narrow endemic serpentine-tolerant species.

Location: We focused on three endemic species with a very limited distribution in the Serra de Careón ultramafic outcrop, a regional plant biodiversity hotspot in Spain.

Methods: We developed SDMs based solely on remotely sensed descriptors of plant water content and habitat dynamics estimated from multitemporal Sentinel 2 images.

Results: The predictive capacity of the models was very high (area under the receiver operating characteristic curve (AUC) > 0.9, sensitivity > 90 and specificity > 84), even for projections beyond the range of data used for calibration (AUC > 0.8, sensitivity > 77 and specificity > 81). Overall, the suitable habitat areas predicted by the models were similar for all three species (Schoener's D metric > 0.7). The annual mean and coefficient of variation of the Normalized Difference of Water Index provided a good representation of the hydromorphic soils with serpentine clay minerals and characterized by the formation of temporary pools during winter months. The annual mean and coefficient of variation of the Modified Soil Adjusted Vegetation Index were also important predictors owing to their capacity to capture the serpentine habitat conditions, characterized by open vegetation and highly exposed soil.

Conclusions: These findings confirm the potential of ecosystem functioning descriptors derived from spectral Sentinel 2 indices as a cost-effective means of characterizing the ecological niche of endemic plant species in serpentine habitats and as a promising tool to support their conservation and monitoring.

KEYWORDS
Armeria merinoi, fine-scale habitat mapping and modelling, *Leucanthemum gallaecicum*, model-based endemic plant monitoring, remotely sensed ecosystem functioning attributes (RS-EFAs), *Santolina melidensis*, serpentine hotspot

1 | INTRODUCTION

Biodiversity is declining at unprecedented rates (Díaz et al., 2019). Habitat loss, degradation and fragmentation are the main drivers of this global crisis because they cause loss of the species associated with these habitats (García, 2011; Santos & Tellería, 2006). To face this massive species loss and contribute to the Aichi Biodiversity Targets proposed by the Convention on Biological Diversity (UNEP, 2010), up-to-date information on biodiversity status and trends is required. Nevertheless, biodiversity is not distributed evenly across the globe. Areas that concentrate significant levels of biodiversity, endemic and endangered taxa have been identified as biodiversity hotspots at both global and regional levels and are considered high-priority target areas for habitat protection and conservation (Kareiva & Kareiva, 2017; Marchese, 2015; Myers et al., 2000). Although the causes of the uneven distribution of biodiversity remain a matter of debate (Merritt et al., 2019), the evolutionary uniqueness that characterizes biodiversity hotspots stems from a particular history shaped by climatic and geological factors. Thus, the concentration of plant biodiversity in regions with unusual geology can be related to habitat heterogeneity and distinct evolutionary pressures due to dramatic shifts in soil conditions, as in the case of ultramafic outcrops. Natural areas with ultramafic geology and serpentine soils are rare, covering less of 1% of the Earth's surface, but frequently harbour distinctive flora and large numbers of endemic species (Brooks, 1987), and are thus considered plant biodiversity hotspots (Harrison & Inouye, 2002). Serpentine soils exert strong selective pressures on plants due to Ca deficiency, high concentrations of Mg and heavy metals (particularly Ni), and a low water-holding capacity (Kruckeberg, 1984). These unique conditions lead to local adaptations and the formation of soil ecotypes, promoting speciation and higher endemic ratios than in surrounding areas (Anacker, 2014). Endemic taxa in serpentine hotspots are likely to have narrow distributions and to be represented by small isolated populations with high levels of inbreeding, resulting in vulnerability to stochastic events and increased extinction risk (Anacker, 2014).

The main tools used to protect threatened endemic species consist of conservation and management plans, which require accurate and up-to-date knowledge about species distribution and habitat status (i.e. monitoring programmes). However, long-term monitoring schemes are very expensive and time-consuming, while management and conservation resources are often limited. Alternative monitoring protocols supported by models have emerged in recent years with the aim of overcoming these limitations (Honrado et al., 2016). Species distribution models (SDMs), which quantify relationships between the environment and the occurrence of species by characterizing the ecological niches (Elith & Leathwick, 2009), enable the creation of predicted distribution maps, despite the limited availability and abundance of species distribution data (Rodríguez et al., 2007). SDMs have been widely used to assess species response to climate and land-use change, support sampling strategies for rare and endangered species and identify priority conservation areas, among other uses (see Elith & Leathwick, 2009; Rodríguez et al., 2007; Villero et al., 2017 and references therein). These modelling techniques have been applied to narrow serpentine endemics to predict species distributions under current or past climatic conditions (Oberprieler et al., 2014). However, these cases rely on climatic envelopes inferred from coarse resolution environmental information, resulting in geographically overestimated predictions of habitat suitability. These techniques perform well at broad geographic scales, but are not considered appropriate for modelling narrow endemics with few spatially distributed occurrences (Gonçalves et al., 2016; Vila-Viçosa et al., 2020). Climatic and edaphic factors interact to control serpentine endemism (Anacker & Harrison, 2012; Fernandez-Going et al., 2013), but identification of fine-scale habitat variables that correctly characterize the niche requirements of target serpentine-tolerant species is challenging.

Satellite-based Earth Observation (EO) has been explored as a very promising tool to support biodiversity mapping and monitoring and thus make advancements in the Aichi Biodiversity Targets (Álvarez-Martínez et al., 2018; Pérez-Silos et al., 2019). The major benefits of using EO data include repeatable coverage allowing for consistent and synoptic monitoring of otherwise inaccessible areas (O'Connor et al., 2015). EO data have increasingly been used to build SDMs based on remotely sensed descriptors of ecosystem functioning (defined as the collective effect of multiple ecosystem processes that determines the exchange of matter and energy between the land surface and atmosphere; Hooper et al., 2005). The incorporation of remotely sensed ecosystem functioning attributes (EFAs) in SDMs has gained attention in recent years (Alcaraz-Segura et al., 2017; Arenas-Castro et al., 2019; Cabello et al., 2012; Regos, Gómez-Rodríguez, et al., 2020; Requena-Mullor et al., 2014). The Copernicus Sentinel 2 mission comprises a constellation of two polar-orbiting satellites (Sentinel 2A and Sentinel 2B) developed by the European Space Agency to monitor land surface conditions. These satellites display improvements over other satellite missions such as SPOT and Landsat, providing complete coverage of the Earth every 5–10 days at higher spectral and spatial resolution (Astola et al., 2019; Mandanici & Bitelli, 2016; Martimort et al., 2007). Despite the most recent advances, little is known about how the Copernicus Sentinel 2 mission can contribute to the fine-scale habitat monitoring of narrow plant endemics in habitats with low plant coverage, such as serpentine soils and alpine areas.

This study aims to assess, for the first time, the potential of remotely sensed descriptors of water and carbon cycles derived from multitemporal Sentinel 2 images for fine-scale habitat characterization and mapping of narrow endemic species in serpentine areas, thus overcoming the problems associated with modelling narrow ranged taxa from intermingled habitats associated with patchily distributed soils (Rodríguez Oubiña & Ortiz, 1991). For this purpose, we modelled three plant species with very limited distributions, considering microhabitat differences in the same serpentine-tolerant endemic plant community. Given the preference of some of the target species for open scrub formations developed on shallow serpentine soils, we expect that remotely sensed variables of intra-annual vegetation dynamics (as a proxy for primary productivity) will be good predictors of habitat quality and distribution. We also hypothesize that, given the preference of the other target species for temporary wet clay and shallow serpentine soils, remote sensing descriptors of water balance would enable accurate characterization of the microhabitat conditions. Thus, SDMs based exclusively on remotely sensed ecosystem functioning variables derived from multitemporal Sentinel 2 images would enable fine-scale characterization and mapping of these habitats. The SDMs would thus be able to accurately predict changes in the habitats and distributions both within and beyond the range of data used for calibration (i.e. strong model performance and transferability). In addition, we expect a large degree of overlap between the ecological niches of the three species but with small differences in the relative importance of each predictor variable according to the microhabitat preferences and ecological requirements (niche) of each target species.

2 | METHODS

2.1 | Study area and species

The study area encompasses the Melide ultramafic outcrop and surrounding areas, which form part of the Capelada-Serra do Careón geological complex, one of the three main ultramafic outcrops in the Iberian Peninsula, together with the Bragança-Morais (Trás-os-Montes, northeast Portugal) and Sierra Bermeja outcrops (Andalusia, southern Spain) (Cerdeira-Pérez et al., 2019). Biogeographically, the study area belongs to the European Atlantic province (Rivas-Martínez et al., 2017), which is characterized by a mild, humid climate (Pardo et al., 2018). Most of the ultramafic outcrop and the species are included in the "Serra do Careón" Natura 2000 network site, which covers an area of 6,665 ha and is protected by the Xunta de Galicia (government of the autonomous region of Galicia). However, a large part of the *Armeria merinoi* population falls outside the protected area (Figure 1). Despite legal protection, the area has undergone continual degradation during the past 20 years, mainly due to fast-growing tree plantations (such as *Eucalyptus* and pine plantations), pasture and forage crops, intensive pig farms, (ultra) mafic quarries and the construction of road infrastructures that have disturbed and fragmented the natural habitats, reducing the populations of the species (Carbajal et al., 2009; Serrano et al., 2009).

We selected three endemic serpentine-tolerant species with very limited distributions as model species: (1) *Santolina melidensis* (Rodr. Oubiña & S. Ortiz) Rodr. Oubiña & S. Ortiz (Asteraceae), which occurs in dry habitats. This species is probably a "budding neo-endemism" that has arisen from a peripheral population of the more widely distributed, closely related *Santolina semidentata*; (2) *Leucanthemum gallaecicum* Rodr. Oubiña & Ortiz (Asteraceae), which shares a habitat with the previous species but is also found in more mesic conditions; and (3) *Armeria merinoi* (Bernis) Nieto Fel. & Silva Pando (Plumbaginaceae), which is located in temporary wet clay and shallow serpentine soils. This habitat type could be included in the "Mediterranean temporary ponds" type of the European Union Habitats Directive, holding priority conservation status (Evans, 2006). Armeria merinoi is one of the few true hygrophilous serpentine-tolerant endemics, apparently being an "insular" neo-endemic species related to alpine *Armeria* species from the northwestern Iberian Peninsula (Nieto Feliner, 1987). The three species are found in close proximity and despite differences in their microhabitats, all three are considered characteristic of the serpentine-endemic *Sagino merinoi-Plantago radicatae* plant community (Rodríguez Oubiña & Ortiz, 1991). All three are currently threatened by loss and degradation of their habitat, with IUCN conservation status reported as "critically endangered" in the case of *A. merinoi* and *S. melidensis*, and as "endangered" in the case of *L. gallaecicum* (Moreno, 2008). The species are legally protected under the Galician Catalogue of Endangered Species within the "endangered" category, obliging the regional government to implement specific management and conservation plans.

2.2 | Modelling framework

As detailed below, we developed SDMs based exclusively on intra-annual descriptors of water balance and habitat dynamics estimated from Sentinel 2 images (rather than a habitat detection approach based on image classification methods). We applied a wide range of modelling techniques and a subset of training data to consider the inherent uncertainty associated with the algorithm and data source. SDMs were validated with cross-validation procedures, and their temporal projections were validated with independent data (to assess the capacity of the models to predict the species distribution beyond the range of data used to calibrate the models; i.e. the temporal transferability). In addition, we quantified the relative importance of each predictor variable and the overlapping of suitable habitat predicted for each target species. Our model-based mapping framework was recently implemented by the regional government in the context of the conservation plans for these endangered species.

2.2.1 | Remotely sensed ecosystem functional attributes

The ecosystem functioning descriptors were computed from images provided by the multispectral instrument aboard the Sentinel 2 satellite of the European Space Agency in 2018 and 2019. We downloaded four satellite images per year (a cloudless image for each season to capture most of the variability in species habitat dynamics throughout each year) from the US Geological Survey (https://earthexplorer.usgs.gov/), with dates as close as possible in each year (22 February 2018, 10 May 2018, 21 August 2018, 14 November 2018, 24 February 2019, 13 May 2019, 3 August 2019, 4 November 2019). All images downloaded were level-1C products, projected in cartographic geometry WGS 84 datum, UTM projection, Zone 29 North. To maximize the usefulness of the data from a multitemporal viewpoint, accurate radiometric calibration and correction procedure is

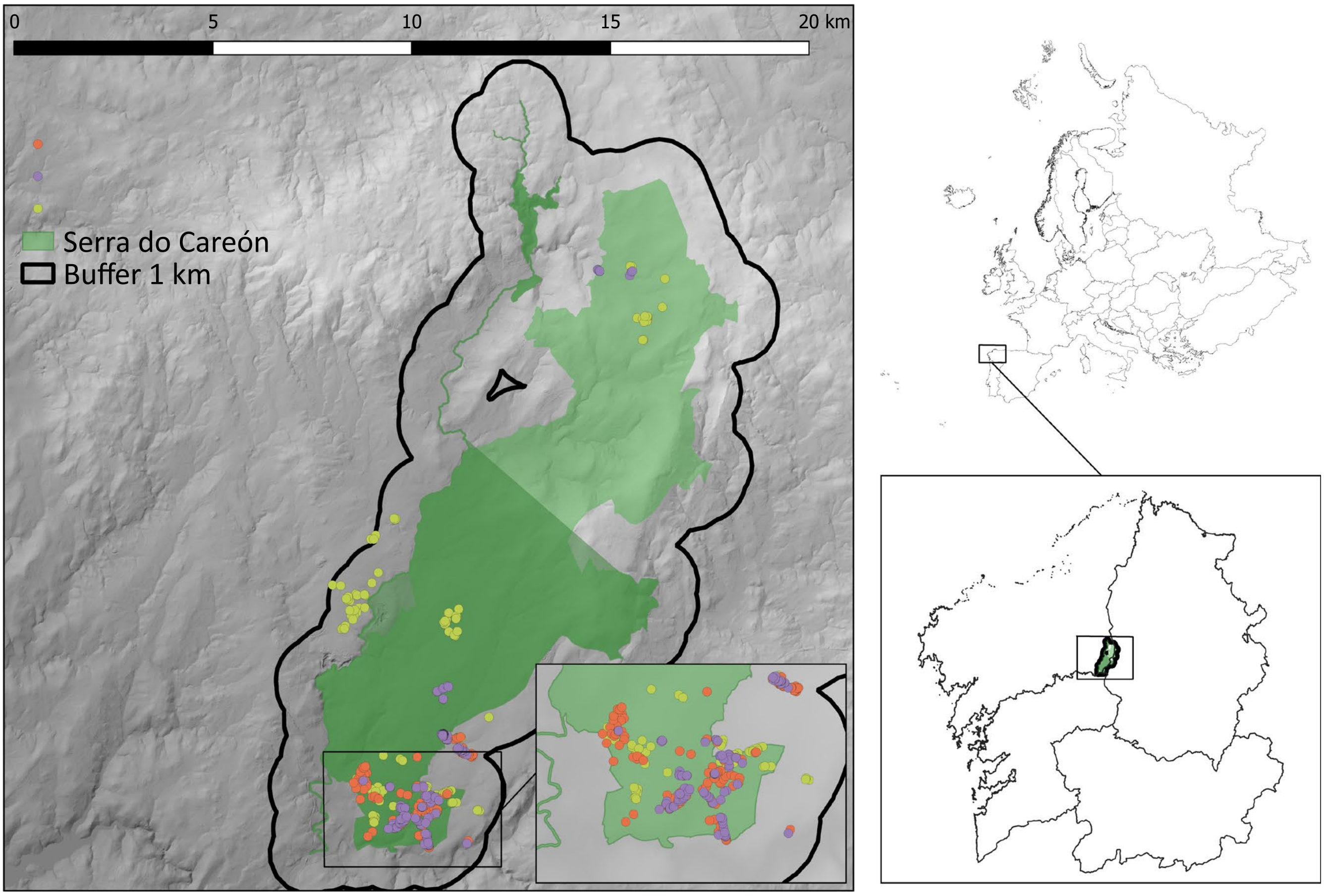

FIGURE 1 Location of the ‘Serra do Careón’ study area in Galicia (Southern Europe). Spatial distribution of all observations of the three target species in the study area

required. Radiometric corrections are necessary due to variations in the illumination and in the geometry of the landscape views, atmospheric conditions, noise and sensor response. Where possible the data should be converted and calibrated with a known (absolute) radiation unit or reflection to facilitate comparison. We corrected each image radiometrically following the dark object subtraction method (Chavez, 1996). This correction method is the most widely used to detect land-use changes. If a dark object (water, forests or shadows) is found in the image, the minimum reflectance value in the histogram is assigned to the object. Using this minimum, it is possible to correct the entire scene by the effects of the atmospheric dispersion. Both calibration and radiometric correction procedures were carried out with the Semi-Automatic Classification plugin developed by Congedo (2013) and included in QGIS software (version 3.14).

After pre-processing the images, we computed five spectral indices for the years 2018 and 2019, with the R package “RStoolbox” (R Core Team, R Foundation for Statistical Computing, Vienna, AT): the Normalized Difference Vegetation Index (NDVI), the Enhanced Vegetation Index, the Modified Soil Adjusted Vegetation Index (MSAVI2), the Normalized Difference Water Index (NDWI) and The Normalized Difference Water Index 2 (NDWI2) (Appendix S1). We then calculated the following metrics from the multitemporal images of each spectral index, for each year and each ecosystem functioning descriptor: annual mean, seasonal coefficient of variation (cv), standard deviation (*SD*), maximum (max), minimum (min) and range (Table 1). These variables are expected to be ecologically meaningful for the target species as they enable fine-scale characterization of the intra-annual habitat dynamics (Carbajal et al., 2009; Serrano et al., 2009). To avoid the use of highly correlated variables in model fitting, we conducted a multicollinearity analysis using the Spearman’s correlation coefficient and the Variable Inflation Factor (VIF) (Alvarez-Martínez et al., 2015). For the final set of predictors used in model calibration (Table 1), the inclusion criteria were Pearson’s correlation coefficient $< |0.7|$ and VIF < 0.3 (Appendix S1).

2.2.2 | Model fitting and evaluation

The models were calibrated using six widely used algorithms available in the R package “biomod2” (R Core Team, R Foundation for Statistical Computing, Vienna, AT), with default settings: generalized linear models, generalized additive models (GAM), generalized boosted models, multivariate adaptive regression splines, random forest and artificial neural networks. We applied a repeated split-sample procedure, using 70% of the initial data for calibration and the remaining 30% for validation (hereafter “cross-validation”). We

TABLE 1 Final set of remotely sensed predictors used for modelling species distributions

Predictor	Abbreviation	Description
NDWI coefficient variation	NDWI_cv	Descriptor of the intra-annual variation in surface waters
NDWI mean	NDWI_mean	Descriptor of annual total amount of surface waters
NDWI2 coefficient variation	NDWI2_cv	Descriptor of seasonal differences in water content of vegetation
NDWI2 minimum	NDWI2_min	Descriptor of minimum extreme of water content of vegetation
MSAVI2 coefficient variation	MSAVI2_cv	Descriptor of seasonality in primary productivity
MSAVI2 mean	MSAVI2_mean	Descriptor of annual total amount of primary productivity

repeated the procedure 10 times (hereafter "runs") to yield predictions accounting for the variability derived from the different training data sets. Because these modelling algorithms required pseudo-absences, we followed the standard procedure (see recommendations in Barbet-Massin et al., 2012) and randomly selected 1,000 pseudo-absences from a large data set (10,000). We avoided potentially suitable areas when creating pseudo-absences by establishing a minimum distance to the presence point of 500 m (Alvarez-Martínez et al., 2015). In addition, we ran each model 10 times by using different randomly selected samples of pseudo-absences to address the potential bias in the spatial distribution (i.e. 6 modelling techniques × 10 runs from the split-sample procedure × 10 pseudo-absences subsets, totalling 600 models for each species). We used four widely accepted metrics to evaluate the model performance: the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), the sensitivity (i.e. the percentage of correctly predicted presences) and the specificity (i.e. the percentage of correctly predicted absences). We also computed an ensemble model from the single-model projections to deal with the inherent uncertainty of individual models and thus provide more informative and ecologically correct predictions (Araújo & New, 2007). Specifically, we used a weighted average approach to construct the ensemble model. This consensus method considers the weights proportional to the selected evaluation scores (i.e. the higher the AUC, the greater the contribution to the ensemble model) (Marmion et al., 2009). Individual models with AUC values higher than 0.9 were selected due to the high observed predictive capacity. Finally, the ensemble models were projected to the environmental conditions for both years considered (2018 and 2019) to assess changes in habitat suitability (Figure 2).

The species occurrences used in this study represent the complete range of the species. The three species are regionally regarded as important for biodiversity conservation in Galicia and have been surveyed by several research teams and conservation management services during the past two decades (Carbajal et al., 2009; Serrano et al., 2009), and thus their actual distribution is well known. Nevertheless, a twin approach was used to increase the accuracy of the study. First, all previously known populations were visited during 2018 and 2019 to verify the current geographical extension and update their boundaries. Second, a systematic sampling scheme was used in all other areas where none of the species have been recorded previously, with only a few fenced private areas excluded in the sampling design. The systematic scheme used the boundaries of the serpentine outcrop in QGIS version 3.14 to define inside a grid of squares with sides of 500 m, with each vertex representing a sampling point. Points at a distance of less than 200 m around a known occurrence of the species were excluded from the systematic scheme as these areas had already been sampled in the first approach to verify the presence of known populations. Some sampling points could not be visited due to restricted access to private land, or because encroaching shrub vegetation hampered access to the exact point location.

Model performance (for both single and ensemble models) was tested using cross-validation procedures. In addition, to test the model transferability (i.e. the model's ability to extrapolate predictions of habitat suitability in time), the model predictions were validated with an independent data source (data from outside the range used to calibrate the models). Models for *L. gallaecicum* and *S. melidensis* were calibrated using field data from 2018 and they were independently validated with field data from 2019. However, because occurrence data for *A. merinoi* were only available for 2019 and not for 2018, models for this species were calibrated with data from 2019, while historical records (gathered from field surveys carried out before 2010) were used for independent validation of the 2018 data that confirm the species occurrence at each location in 2019 (and therefore also in 2018) (Table 2).

We calculated the relative importance of each predictor to explain the distribution of each target species by using the "variables_importance" function available in the R package "biomod2" (R Core Team, R Foundation for Statistical Computing, Vienna, AT). The procedure uses Pearson's correlations between the standard predictions (i.e. fitted values) and predictions where the variable under investigation has been randomly permutated, in a procedure that is repeated 10 times for each variable. We calculated the sum of variable importance across models and replicates to consider the relative importance of different groups of variables. Results were plotted with the R package "ggplot2" (R Core Team, R Foundation for Statistical Computing, Vienna, AT) (Wickham, 2016). To compare the habitat suitability maps predicted by our models for the three species, we calculated the Schoener's D metric, the most common measure of niche overlap (Broennimann et al., 2012; Schoener, 1970), with the "nicheOverlap" function available in the R package "dismo", version 1.1-4 (R Core Team, R Foundation for

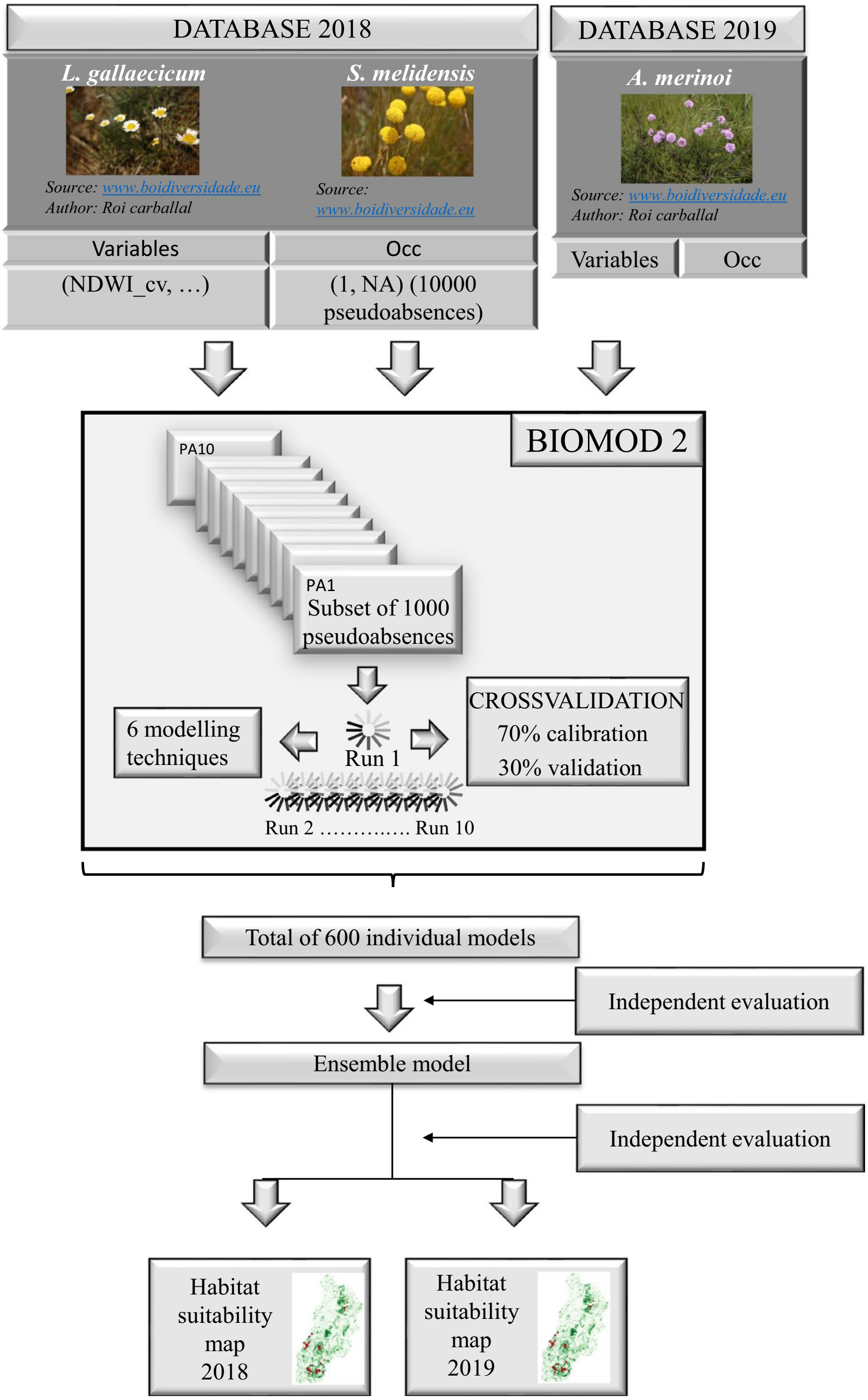

FIGURE 2 Flowchart of the model fitting and evaluation

Statistical Computing, Vienna, AT). We also calculated the difference in habitat suitability (expressed in %) between 2018 and 2019. The resulting maps enable identification of the areas most affected by habitat changes during the two years (Appendix S2). In addition, we created a BAM diagram as an abstract representation of the geographical space, adapted from Alvarez-Martínez et al. (2015), to illustrate the contribution of our modelling framework to the ecological niche characterization of each target species in relation to the other species.

3 | RESULTS

3.1 | Model performance and transferability

The ensemble models yielded a very high predictive accuracy for all species in both the cross-validation (AUC of 0.990 for *L. gallaecicum*, 0.992 for *S. melidensis* and 0.969 for *A. merinoi*) and independent validation procedures (AUC of 0.904 for *L. gallaecicum*, 0.958 for *S. melidensis* and 0.962 for *A. merinoi*). They also performed well for all species with the TSS metric in cross-validation procedure (TSS of 0.942 for *L. gallaecicum*, 0.938 for *S. melidensis* and 0.836 for *A. merinoi*), although a moderate decrease was observed when tested against independent data (TSS of 0.479 for *L. gallaecicum*, 0.739 for *S. melidensis* and 0.858 for *A. merinoi*).

Overall, single-algorithm models performed well in the cross-validation procedure (mean AUC values > 0.8), with the best results yielded by the random forest and generalized boosted model algorithms (Figure 3). In particular, models yielded AUC values of 0.929 ± 0.050 for *L. gallaecicum* (sensitivity of 91.788 ± 9.439, specificity of 89.218 ± 5.310), 0.951 ± 0.034 for *S. melidensis* (sensitivity of 93.142 ± 6.446, specificity of 91.194 ± 4.227) and 0.929 ± 0.022 for *A. merinoi* (sensitivity of 90.666 ± 5.478, specificity of 84.822 ± 5.094) (see Table 3 and Appendix S1). The model performance remained high even when projected to environmental conditions beyond the range of data used for calibration (see independent validation for *A. merinoi* and *S. melidensis* in Figure 3), with AUC values of 0.836 ± 0.062 for *L. gallaecicum* (sensitivity of 77.416 ± 12.701, specificity of 81.573 ± 6.413), 0.915 ± 0.048 for *S. melidensis* (sensitivity of 86.612 ± 8.384, specificity of 87.606 ± 3.450) and 0.937 ± 0.025 for *A. merinoi* (sensitivity of 95.441 ± 4.486, specificity of 85.362 ± 5.838) (see Table 3 and Appendix S1).

TABLE 2 Final number of presences used to model each species after controlling for pseudo-replication (i.e. after removal of presences recorded within the same pixel of the image)

Species	2018	2019
Leucanthemum gallaecicum	50	81
Santolina melidensis	69	111
Armeria merinoi	20	136

3.2 | Variable importance and spatial patterns

The NDWI annual mean (descriptor of annual surface water balance) was the most important predictor for the three species, although in *A. merinoi* the MSAVI2 annual coefficient of variation (descriptor of seasonality of primary productivity) was of similar importance (Figure 4). The coefficients of variation and annual minimum of

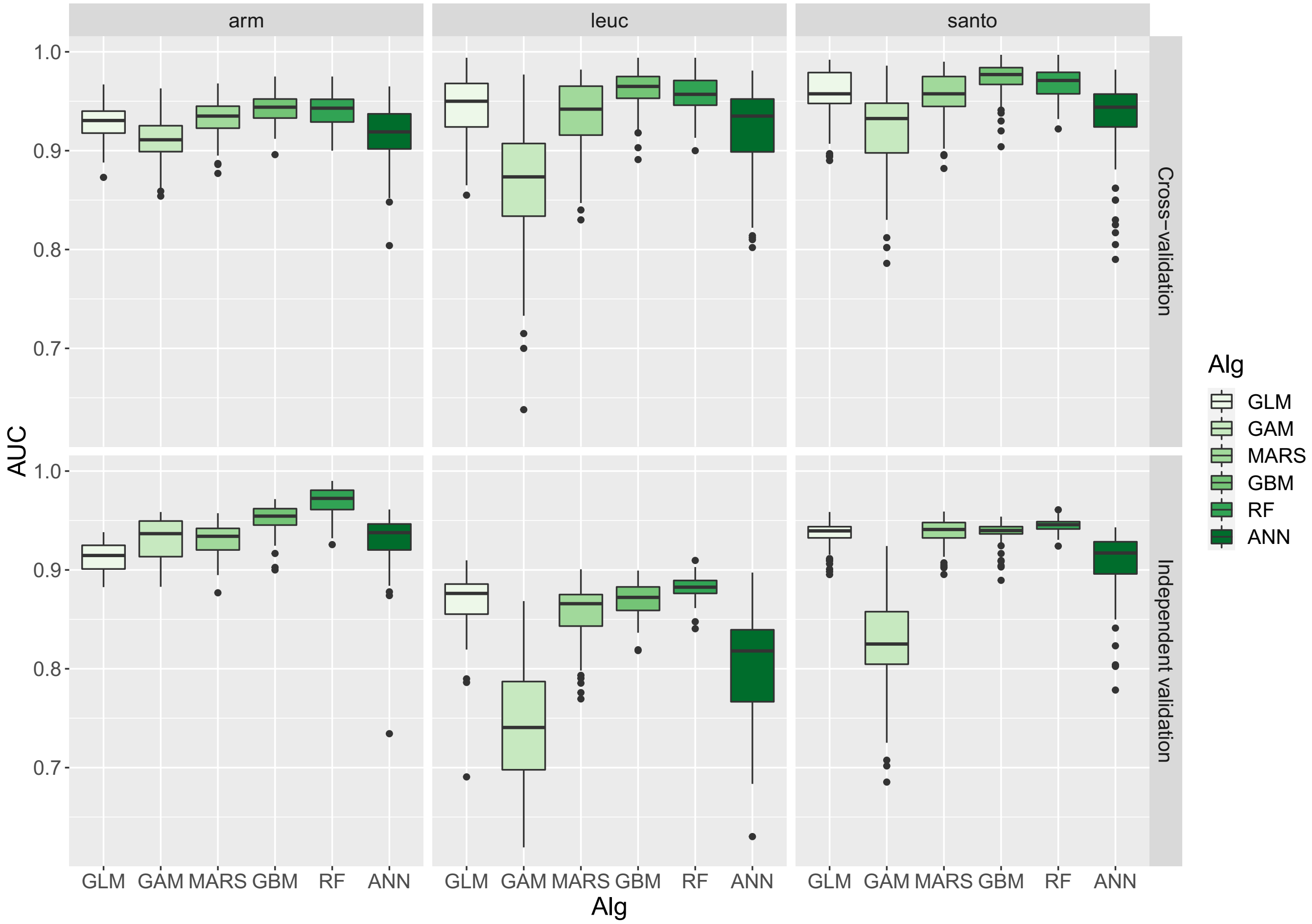

FIGURE 3 Area under the curve (AUC) for individual models by species, algorithm and type of validation. *Armeria merinoi*: 'arm', *Leucanthemum gallaecicum*: 'leuc' and *Santolina melidensis*: 'santo'. See abbreviations for the different algorithms in 'Model fitting and evaluation'. The median is represented by the central lines, delimiting the first and third quartiles. Whiskers extend to extreme values and outliers are represented by black dots

TABLE 3 Mean and standard deviation across modelling techniques and replicates for the area under the receiver operating characteristic curve (AUC) with the sensitivity and specificity metrics, for both cross-validation and independent validation

Species	AUC	Sensitivity	Specificity
Cross-validation			
Leucanthemum gallaecicum	0.929 ± 0.050	91.788 ± 9.439	89.218 ± 5.310
Santolina melidensis	0.951 ± 0.034	93.142 ± 6.446	91.194 ± 4.227
Armeria merinoi	0.929 ± 0.022	90.666 ± 5.478	84.822 ± 5.094
Independent validation			
Leucanthemum gallaecicum	0.836 ± 0.062	77.416±12.701	81.573 ± 6.413
Santolina melidensis	0.915 ± 0.048	86.612 ± 8.384	87.606 ± 3.450
Armeria merinoi	0.937 ± 0.025	95.441 ± 4.486	85.362 ± 5.838

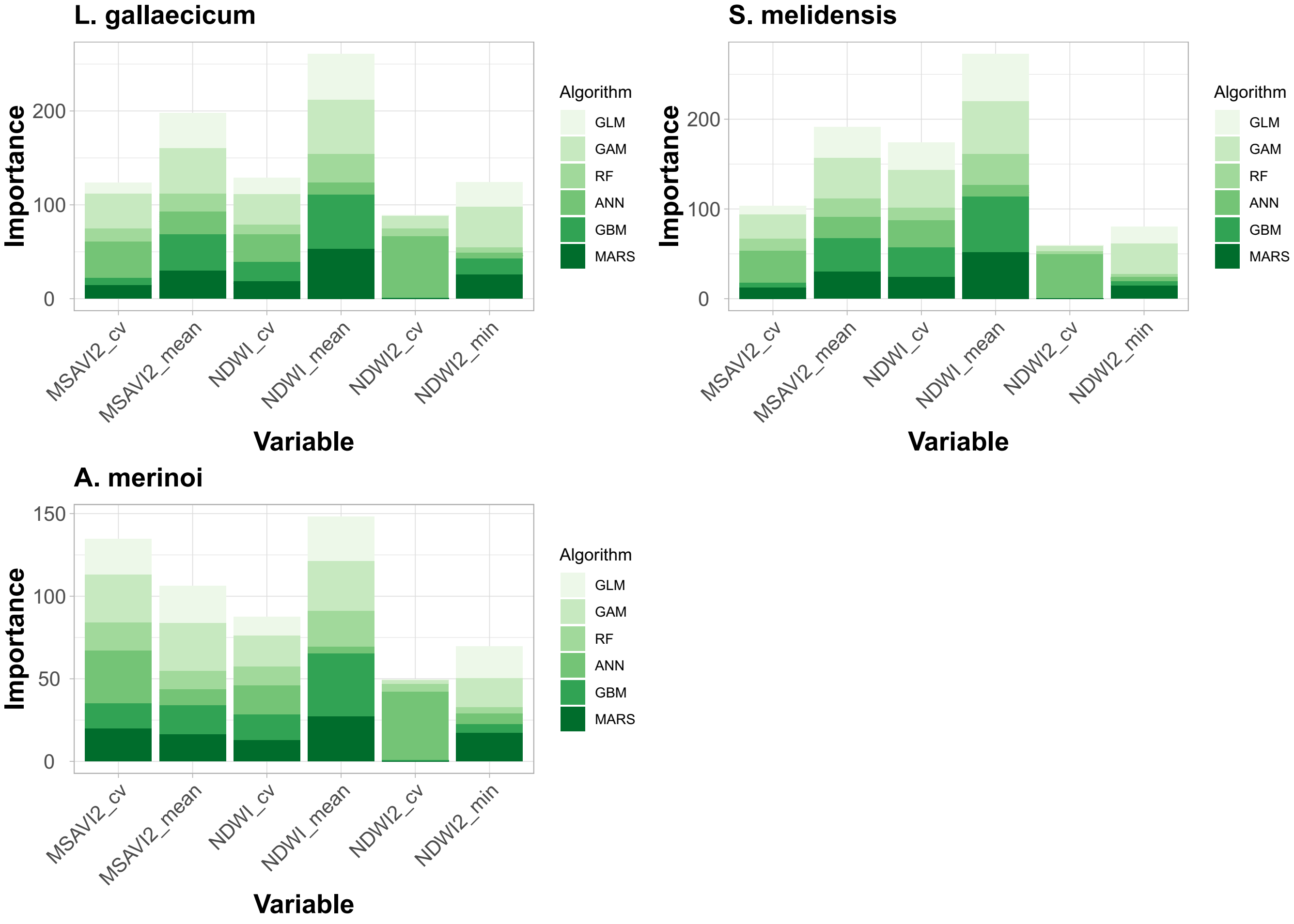

FIGURE 4 Variable importance of each target species resulting from cumulative sums across the different species, modelling algorithms and replicates. See abbreviations for the different algorithms in 'Model fitting and evaluation' and for the predictor variables in Table 1

NDWI2 (descriptors of seasonality and minimum extreme values of water content of vegetation respectively) were the least important variables for *S. melidensis* and *A. merinoi*, whereas for *L. gallaecicum* they were as important as the coefficients of variation of MSAVI2 and NDWI (descriptors of seasonality in primary productivity and surface water balance, respectively) (Figure 4). The differences in values of importance of the four main predictors for *A. merinoi* (NDWI mean = 145, MSAVI2 cv = 130, MSAVI2 mean = 105 and NDWI cv = 85) are markedly lower than for *S. melidensis* (ranging from NDWI mean = 270 to MSAVI2 cv = 105) and *L. gallaecicum* (ranging from NDWI mean = 260 to MSAVI2 cv = 115), with these variables showing a more equilibrated contribution in the models developed for the former species (Figure 4).

The habitat projections obtained from the ensemble SDMs showed high habitat suitability in areas where the species were found in both years. Overall, the suitable habitat areas predicted by our models were similar for all three species, being most similar for *L. gallaecicum* and *S. melidensis*, whereas *A. merinoi* showed a broader potential distribution (Figure 5, Table 4). In addition, a slight increase in habitat suitability was predicted for 2019 relative to the

FIGURE 5 Habitat suitability maps for the species in 2018 (upper) and 2019 (lower). Dark green areas indicate high habitat suitability. Circles indicate zones where there have been marked changes in the habitat suitability among years. The coloured dots represent species presence points

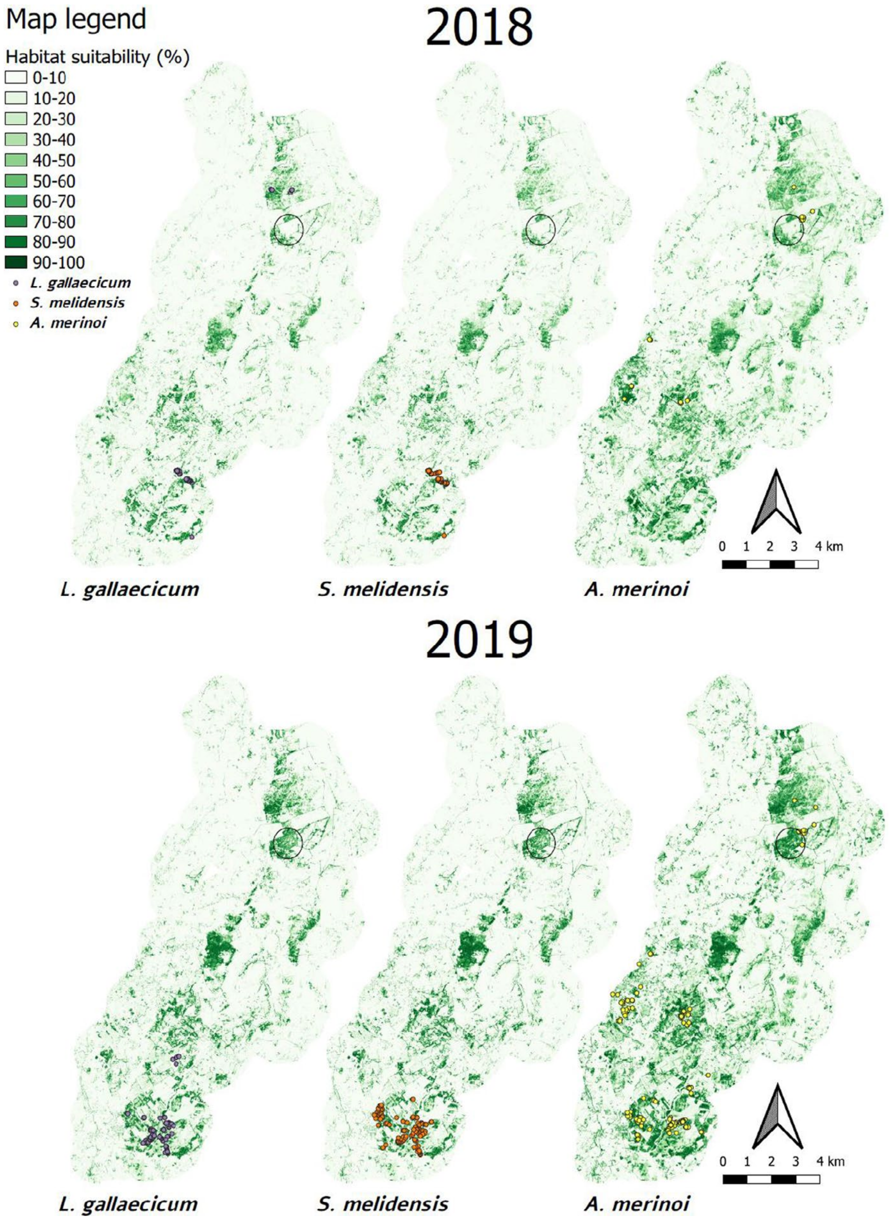

TABLE 4 Overlap in habitat suitability between species in both years measured by the Schoener's D metric

	Armeria merinoi–Leucanthemum gallaecicum	*Armeria merinoi–Santolina melidensis*	*Leucanthemum gallaecicum–Santolina melidensis*
2018	0.745	0.737	0.891
2019	0.782	0.760	0.921

habitat suitability maps for 2018; up to 15.43% for *L. gallaecicum*, 17.45% *for S. melidensis* and 11.22% for *A. merinoi* (Appendix S2).

4 | DISCUSSION

Our SDMs based exclusively on multitemporal images of Sentinel 2 displayed very good predictive capacity, supporting their use for habitat monitoring for narrow endemic plant species and vegetation in ultramafic outcrops. The study findings confirm the potential value of the EFAs measured from remote-sensing products as a cost-effective means of fine-scale habitat mapping and characterization based on the ecological requirements (niche) of endangered endemic plant species in serpentine soils, as observed previously for other species with different ecologies (Alcaraz-Segura et al., 2017; Arenas-Castro et al., 2019; Requena-Mullor et al., 2014; Wiegand et al., 2008).

4.1 | Sentinel-based models of endemic plant distributions

Although the target species are perennial, and thus characterized by low inter-annual geographic variation, the predictive capacity of the models was very high, even when projected to different environmental conditions (i.e. beyond the range of data used for model calibration; see AUC values in Figure 3). Overall, the modelling algorithms provided very good predictions, except for the GAMs, which require fine-tuning (Hao et al., 2020). The models showed a lower capacity to correctly predict absences compared with presences (i.e. very high sensitivity, but lower specificity values), which could potentially lead to overestimation of the range of distribution (Alatorre & Beguería, 2009) (see Figure 5 and Appendix S1). In addition, the theorical independence of prevalence of accuracy metrics such as sensitivity, specificity, TSS and AUC may be questioned in real-world applications, indicating the need for caution when using model predictions for management purposes (Foody, 2011). Nonetheless, the rates of omission/commission errors of our model predictions were low (sensitivity and specificity > 0.7) when tested with truly independent data, confirming the high predictive capacity of the models (see Table 3), except for GAMs of *L. gallaecicum* (see Appendix S2). The ensemble models resulting from the combination of all techniques showed greater predictive capacity than the single-algorithm models (see Section 3.1 and Table 3), as already widely demonstrated in previous studies (Araújo & New, 2007; Thuiller et al., 2009).

The habitat suitability projections were similar for the three species (Table 4, Appendix S2), with large areas predicted as suitable habitat in the northern zone of the study area, where *L. gallaecicum* and *A. merinoi* occur. None of the species have been recorded in the middle zone of the study area, although relatively well-conserved areas of serpentine soils are present (Figure 5). The Serra de Careón outcrop forms a patchy landscape mainly composed of mafic non-serpentine and ultramafic serpentine soils, with the endemic serpentine flora restricted to the latter. Interestingly, the suitability predictions of our SDMs indirectly distinguish between different soil-related habitats, identifying serpentine areas as the most suitable for the species among all other substrates, without any edaphic information having been included in the models (see *Ga* in the BAM diagram, Figure 6). This supports the idea that, at least for the study area, serpentine habitats can be accurately described by spectral indices of local habitat variables, even across within-region climatic gradients. Nevertheless, the fact that none of the three study species have been found in the middle and northeastern zones may be due to their extirpation during the long-established traditional use of the area or due to intrinsic dispersal limitations (*M* in Figure 6), which may have prevented recovery of their putative former range to date.

The absence of *S. melidensis* is less surprising than the absence of *A. merinoi* and especially *L. gallaecicum*, because the middle and northeastern zones are mostly above 730 m a.s.l., which is higher than the upper elevational range of *S. melidensis* (Carbajal & Serrano, 2004). Environmental niche studies in the California serpentine biodiversity hotspot identified a wide elevational range for ultramafic tolerant species according to which serpentine populations are found at lower elevations than non-serpentine populations, at both the low and high extremes of elevation distributions (Burge & Salk, 2014). This pattern has been related to two mechanisms of plant range limitation: a biotic limitation at lower elevations with higher temperatures and evapotranspiration ratios where serpentines would provide refuge for competition; and an abiotic limitation at upper elevations, where the effects of cold temperatures would be exacerbated by the rather infertile serpentine soils (Burge & Salk, 2014; Ettinger et al., 2011). In addition, endemic serpentine-tolerant species would occupy wetter regions than their closest relatives, although only in the case of endemics that have arisen via a neo-endemic pathway (Harrison, 2013). *S. melidensis* fits both patterns, as it belongs to a drought-adapted Mediterranean genus with pioneering ecological behaviour and occurs under the wetter macroclimate of the Atlantic European region (Amigo et al., 2017) than the closely related *S. semidentata* (Carbajal et al., 2019). It is therefore possible that the higher elevations of middle and northern serpentine zones produce microclimatic conditions beyond the environmental envelope of the species (see *M* in Figure 6), which establishes a framework for hypotheses-testing translocation experiments along the altitudinal cline and is particularly interesting in the current context of conservation concerns related to global climatic change.

A. merinoi and *L. gallaecicum* occur at higher elevations in the northern part of the study area. The microhabitat requirements of *A. merinoi* demand thin, although hydromorphic soils with serpentine clays that allow the formation of temporary pools during winter months, whereas *L. gallaecicum* normally occupies drier and rocky serpentine habitats, but also occurs secondarily in disturbed and somewhat mesic environments (e.g. vegetated rural track margins). Traditional agricultural practices may have affected the microhabitat conditions for *A. merinoi* more dramatically than for *L. gallaecicum*, hampering eventual (re)colonization of the area by the former species. *L. gallaecicum* fits this pattern, and species absence might be better explained by dispersal limitations from the remnant southern and northern populations once the middle zone has become surrounded by unsuitable habitat (*Ga* in Figure 6).

4.2 | EFAs as reliable descriptors of endemic plant distributions

Regarding the relative importance of each predictor variable, the annual mean of the NDWI was found to be the most important variable in all models (see Figure 4). Strong selection by serpentine soils creates an evolutionary playground with its own adaptive rules and intrinsic competitive relationships. Stress-tolerance traits include a low growth rate, which is consistent with a trade-off with competitive ability for serpentine tolerance. Thus, the optimal habitat in the study area is a stable (on rocky skeletal soils) community of *Sagino merinoi-Plantago radicatae*, a low coverage of sparse scrubs and herbaceous species with characteristically exposed soils and low competition; this could explain the lower importance of the NDWI2

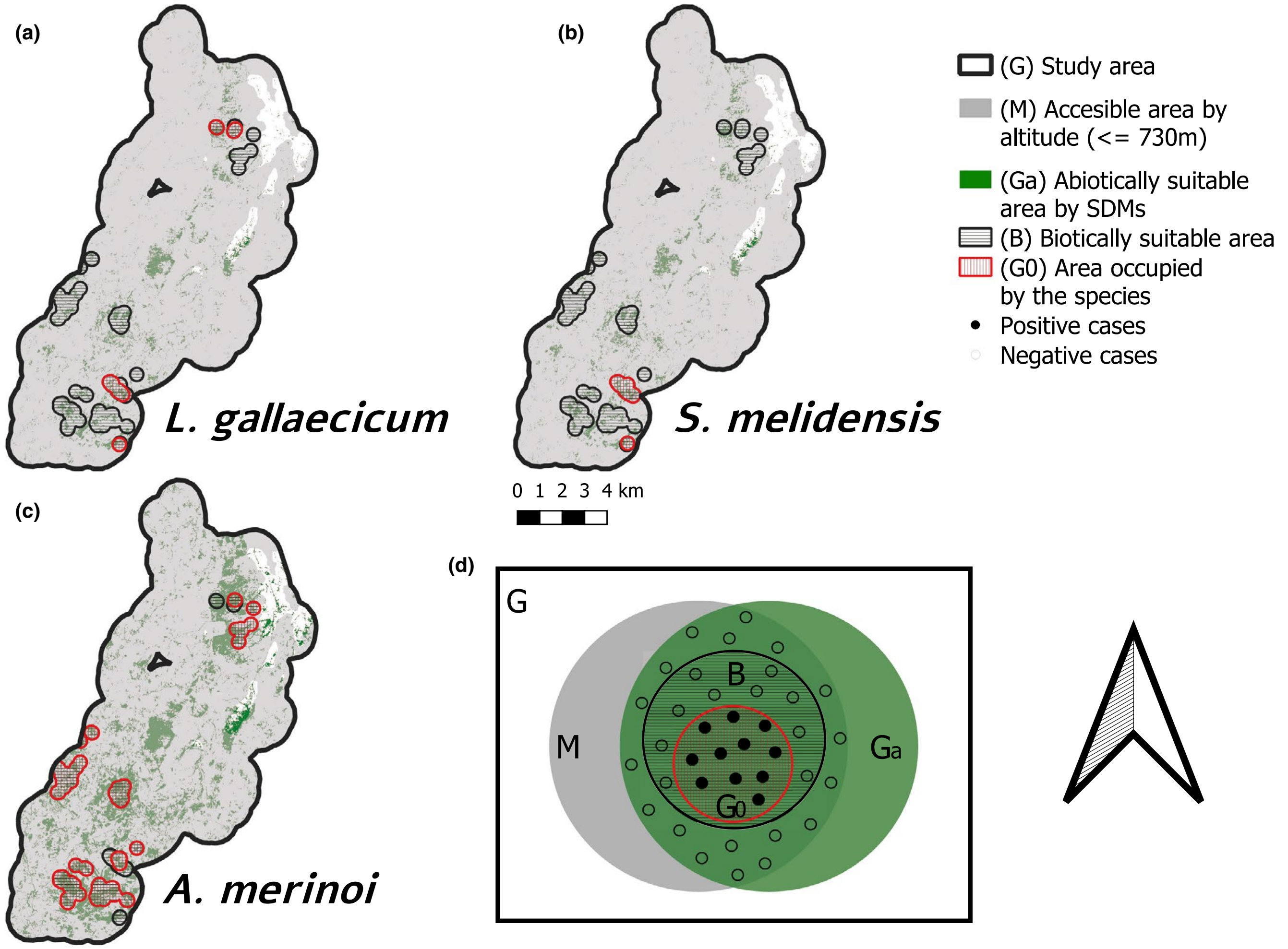

FIGURE 6 BAM diagram adapted from Alvarez-Martínez et al. (2015). Distribution maps for (a) *Leucanthemum gallaecicum*, (b) *Santolina melidensis* and (c) *Armeria merinoi*, corresponding to the BAM diagram. (d) Abstract representation of the BAM diagram. G, study area; M, accessible area at the elevation where the species can be found; Ga, abiotically suitable areas obtained from the species distribution models; B, biotically suitable areas obtained by combining the areas occupied by the three serpentine species; G0, area occupied by each species

than of the NDWI, which makes a greater distinction between vegetation, soil and water bodies (McFeeters, 1996). Outside the best-conserved areas with skeletal soils, the elements of the serpentine community act as pioneer colonizers, only occurring at some track margins or in collapsed traditional serpentine stone walls (Figure 5), a longitudinal pattern captured by our SDM predictions and also a marker of biocultural heritage (Grove et al., 2020). Drought adaptations in the serpentine vegetation include smaller plants and reduced leaf-specific area, which explain the lesser importance of the predictors, as NDWI2 relates to the water content of plants. The descriptors of the water content of vegetation or soil captured by Sentinel 2 images have previously been described as good predictors of habitat quality in vertebrates occurring in more mesic or hygrophilous habitats. For example, the annual standard deviation of the NDWI2 captured by Sentinel 2 proved a good descriptor of the grassland wader habitat, because these species feed in flooded areas where prey are more readily available (Regos, Vidal, et al., 2020). Conversely, the NDWI, together with MSAVI2 and Brightness Index 2 derived from Sentinel 2 images, were also found to be important predictors in relatively xeric sandy habitats and performed well for mapping coastal dune landscapes (Marzialetti et al., 2020), confirming their usefulness for open dry habitats such as the serpentine areas (Delpino Aguayo et al., 2018; Eid et al., 2020; Kaplan & Avdan, 2017).

The set of remote-sensed EFAs enabled us to characterize the habitat preferences at very fine scale for species that share the same broad habitat type but differ in microhabitat requirements. For instance, although *A. merinoi* and *L. gallaecicum* both occupy open scrub formations developed in shallow serpentine soils, *A. merinoi* demands hydromorphic soil, whereas *L. gallaecicum* normally occupies dry, rocky serpentine habitats. This leads to a high degree of niche overlap (see Table 4, and *B* in Figure 6) and similar relative importance of the most important variable (the annual mean of NDWI), but clear differences in the importance of coefficient of variation and annual mean of MSAVI2 (see Figure 4). The ecological relevance of this variable for *L. gallaecicum* and *S. melidensis* can again be explained by the conditions of the serpentine habitats, characterized by open vegetation and highly exposed soil, resulting in low competition and extremely slow growth rate, as identified in a multi-year demographic monitoring of *S. melidensis* (Carbajal et al., 2009). MSAVI2 has been found to be particularly useful in habitats in rocky arid regions (Narayanan et al., 2013; Vanselow & Samimi, 2014). The good performance of this descriptor for the Serra de Careón outcrop (located within the humid Atlantic European biogeographic region) supports the idea that the strong constraints imposed by serpentine soils on the ecosystem shape functionally xeric habitats, with serpentine soil being a more important ecological driver than regional macroclimate. *A merinoi* differed from the other two species in terms of variable importance, because the coefficient variation of the MSAVI2 was of similar importance to the annual mean of NDWI, and the differences in explaining the contribution among the four main predictors were significantly less than in *S. melidensis* and *L. gallaecicum*. *A. merinoi* is mainly found in the dry serpentine community of *Sagino merinoi-Plantago radicatae* that constitutes the endemic-rich habitat of *S. melidensis* and *L. gallaecicum*. Analysis of the serpentine vegetation in the northwestern Iberian Peninsula indicated this species as part of the community of the class Festucetea (Izco Sevillano & Rivas-Martínez, 2018; Rodríguez Oubiña & Ortiz, 1991). However, microtopographic variation leads to rather flat depressions with serpentine clay deposition where water accumulates during the winter. *A. merinoi* occupies these shallow depressions, in which extremely short-living communities of hygrophilous annual species live. Rapid dieback of annual species leaves the perennial *A. merinoi* as one of the few identifiable species remaining during most of the year in dry exposed soils. Although it intermingles with the mostly perennial species of the drier serpentine community, the seasonality of the *A. merinoi* microhabitat was correctly captured by the coefficient of variation of the MSAVI2. The different performance of this predictor for *A. merinoi* suggest that the main habitat of the species probably deserves better characterization to separate it from that of the *Sagino merinoi-Plantago radicatae* community.

The above-reported findings are consistent with those observed for other endemic plant species. A recent study related the presence and abundance of the narrow Iberian endemic "Gerês lily" (*Iris boissieri*) to descriptors of annual primary productivity, specifically the Enhanced Vegetation Index, calculated from data provided by the MODIS sensor of NASA's TERRA satellite (Arenas-Castro et al., 2019). However, in a previous study, the same authors found that remote sensing descriptors related to energy balance (e.g. surface temperature or Albedo) were also good predictors of the distribution of the lily, which invites consideration of other spectral indices from Sentinel 2 that could capture other relevant aspects of the species ecology (Arenas-Castro et al., 2018). In addition, the high potential of passive sensors (e.g. RADAR images captured by the Synthetic Aperture Radar sensor of the Sentinel 1 satellite) for monitoring aquatic environments remains to be explored (Pham-Duc et al., 2017; Yesou et al., 2016). These promising results open up new avenues for supporting the planning and management of endangered plant species in protected areas. Our modelling framework would facilitate the identification of new areas where populations can be reinforced through, e.g. translocation programmes (Guisan et al., 2013). In addition, it would also support adaptive management by monitoring the habitat conditions of these target species in managed areas, e.g. in habitat restoration programmes (Regos, Vidal, et al., 2020).

5 | CONCLUSIONS

Ecosystem functioning descriptors derived from multitemporal Sentinel 2 images enable fine-scale habitat mapping and characterization based on the ecological requirements (niche) of three narrow endemic serpentine plants in a plant biodiversity hotspot in the northwestern Iberian Peninsula. The SDMs developed here, based exclusively on multitemporal Sentinel 2 images, accurately predicted the presence of the target species associated with the remnant zones of well-conserved serpentine soils in the Serra de Careón ultramafic outcrop. The models also captured the habitat envelope characteristics resulting from the strong selective pressures exerted by serpentine soils on plant communities that ultimately govern the emergence and establishment of the serpentine endemic species. This was an unexpected result as the models did not include any edaphic information. In addition, the remote-sensing products enabled the development of SDMs with a high predictive capacity within and beyond the range of data used to calibrate the models, providing a cost-effective alternative to standardized habitat monitoring, although subject to the availability of Sentinel 2 satellite images. These models will also help to prioritize future sampling efforts in those areas predicted to be suitable for the species, but where no populations have yet been detected, as well as to identify potential areas for translocation and population reinforcement. The study findings demonstrate the potential value of remote sensing as a support tool for managers of threatened plant species with narrow distributions in protected areas and biodiversity hotspots where the presence of rare species is related to local and patchy distributed environmental conditions, such as serpentine outcrops and other areas with evolutionary constraining soils. They also demonstrate the advantages of considering variables related to different dimensions of ecosystem functioning (such as water balance and carbon cycle) in addition to more traditional approaches that rely on structural habitat variables or macroclimatic databases and that perform better at broader scales.

ACKNOWLEDGEMENTS

The authors acknowledge the collaboration of the Dirección Xeral de Patrimonio Natural, Xunta de Galicia, for providing some of the *Armeria merinoi* occurrence data used. The *Santolina melidensis* and *Leucanthemum gallaecicum* field surveys were funded by Acciona Construcción in the framework of a recovery plan for the populations of these species affected by construction of the A-54 motorway.

AUTHOR CONTRIBUTIONS

AR conceived ideas and designed the methodology. SP-F and AR performed lead writing and analysis. MS and RC collected data and assisted in the analysis and interpretation. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Because the target species are endangered in our study area, occurrence data are available upon reasonable request to the corresponding author. Environmental variables from Sentinel satellite are freely available from the US Geological Survey (https://earthexplorer.usgs.gov/).

ORCID

Miguel Serrano https://orcid.org/0000-0003-3079-2355
Roi Carballal https://orcid.org/0000-0002-1505-252X
Adrián Regos https://orcid.org/0000-0003-1983-936X

REFERENCES

Alatorre, L.C. & Beguería, S. (2009) *Identificacion de zonas de erosion activa y áreas de riesgo mediante teledeteccion*. Cuadernos de Investigación Geográfica.

Alcaraz-Segura, D., Lomba, A., Sousa-Silva, R., Nieto-Lugilde, D., Alves, P., Georges, D. et al. (2017) Potential of satellite-derived ecosystem functional attributes to anticipate species range shifts. *International Journal of Applied Earth Observation and Geoinformation*, 57, 86–92.

Álvarez-Martínez, J.M., Jiménez-Alfaro, B., Barquín, J., Ondiviela, B., Recio, M., Silió-Calzada, A. et al. (2018) Modelling the area of occupancy of habitat types with remote sensing. *Methods in Ecology and Evolution*, 9, 580–593.

Alvarez-Martínez, J.M., Suárez-Seoane, S., Palacín, C., Sanz, J. & Alonso, J.C. (2015) Can Eltonian processes explain species distributions at large scale? A case study with Great Bustard (*Otis tarda*). *Diversity and Distributions*, 21, 123–138.

Amigo, J., Rodríguez Guitián, M.A., Honrado, J. & Alves, P. (2017) The lowlands and midlands of northwestern Atlantic Iberia. In: Loidi, J. (Ed.) *The Vegetation of the Iberian Peninsula*. volume 1. Cham: Springer International Publishing, pp. 191–250.

Anacker, B.L. (2014) The nature of serpentine endemism. *American Journal of Botany*, 101(2), 219–224.

Anacker, B.L. & Harrison, S.P. (2012) Historical and ecological controls on phylogenetic diversity in Californian plant communities. *American Naturalist*, 180(2), 257–269.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, 22, 42–47.

Arenas-Castro, S., Regos, A., Gonçalves, J.F., Alcaraz-Segura, D. & Honrado, J. (2018) Assessing the multi-scale predictive ability of ecosystem functional attributes for species distribution modelling. *PLoS One*, 13(6), 1–31.

Arenas-Castro, S., Regos, A., Gonçalves, J.F., Alcaraz-Segura, D. & Honrado, J. (2019) Remotely sensed variables of ecosystem functioning support robust predictions of abundance patterns for rare species. *Remote Sensing*, 11(18), 1–16.

Astola, H., Häme, T., Sirro, L., Molinier, M. & Kilpi, J. (2019) Comparison of Sentinel-2 and Landsat 8 imagery for forest variable prediction in boreal region. *Remote Sensing of Environment*, 223, 257–273.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, 3(2), 327–338.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G. et al. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, 21, 481–497.

Brooks, R.R. (1987) *Serpentine and Its Vegetation: a Multidisciplinary Approach*. Portland, OR: Dioscorides Press.

Burge, D.O. & Salk, C.F. (2014) Climatic niche shifts in the serpentine soil flora of California. *Journal of Vegetation Science*, 25(3), 873–884.

Cabello, J., Fernández, N., Alcaraz-Segura, D., Oyonarte, C., Piñeiro, G., Altesor, A. et al. (2012) The ecosystem functioning dimension in conservation: insights from remote sensing. *Biodiversity and Conservation*, 21(13), 3287–3305.

Carbajal, R., Ortiz, S. & Sáez, L. (2019). Santolina L. In Castroviejo, S.B., Benedí, C., Buira, A., Rico, E. & Crespo, M.B. (Eds.), *Flora iberica*, vol. 16(3), pp. 1938–1962. Real Jardín Botánico, CSIC.

Carbajal, R. & Serrano, M. (2004) *Santolina melidensis* (Rodr. Oubiña & S. Ortiz) Rodr. Oubiña & S. Ortiz. In: Bañares, Á., Blanca, G., Güemes, J., Moreno, J.C. & Ortiz, S. (Eds.) *Atlas y Libro Rojo de la Flora Vascular Amenazada de España*. Madrid: Dirección General de Conservación de la Naturaleza, pp. 478–479.

Carbajal, R., Serrano, M., Ortiz, S., Iriondo, J.M. & M. J., A. (2009). Santolina melidensis (Rodr. Oubiña & S. Ortiz) Rodr. Oubiña & S. Ortiz. In Iriondo, J., Albert, M., Giménez Banavides, L., Domínguez Lozano, F. & Escudero, A. (Eds.), *Populations in Peril: Demographic Viability of Threatened Spanish Vascular Flora*, pp. 129–132. Madrid: Medio Natural y Política Forestal (Ministerio de Medio Ambiente, y Medio Rural y Medio Marino).

Cerdeira-Pérez, A., Monterroso, C., Rodríguez-Garrido, B., Machinet, G., Echevarria, G., Prieto-Fernández, Á. et al. (2019) Implementing nickel phytomining in a serpentine quarry in NW Spain. *Journal of Geochemical Exploration*, 197, 1–13.

Chavez, J. (1996) Image-based atmospheric corrections – revisited and improved. *Photogrammetric Engineering & Remote Sensing*, 62, 1025–1036.

Congedo, L. (2013). Semi-Automatic Classification Plugin for QGIS. Technical Report. Rome, Italy.

Delpino Aguayo, M.A., Portillo Sosa, V.M. & Mora Stanley, C.R. (2018) Evaluación de índices espectrales derivados de sensores para la caracterización de ambientes de humedales. In Anais 7 Simpósio de Geotecnologias no Pantanal, Jardim, MS, 20 a 24 de outubro 2018. Embrapa Informática Agropecuária/INPE, pp. 114–121.

Díaz, S., Settele, J., Brondízio, E., Ngo, H.T., Guèze, M., Agard, J. et al. (2019) *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Bonn: IPBES Secretariat.

Eid, A.N.M., Olatubara, C.O., Ewemoje, T.A., El-Hennawy, M.T. & Farouk, H. (2020) Inland wetland time-series digital change detection based on SAVI and NDWI indecies: Wadi El-Rayan lakes, Egypt. *Remote Sensing Applications: Society and Environment*, 19, 100347.

Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 677–697.

Ettinger, A.K., Ford, K.R. & Hille Ris Lambers, J. (2011) Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology*, 92(6), 1323–1331.

Evans, D. (2006) The habitats of the European union habitats directive. *Biology & Environment: Proceedings of the Royal Irish Academy*, 106(3), 167–173.

Fernandez-Going, B.M., Harrison, S.P., Anacker, B.L. & Safford, H.D. (2013) Climate interacts with soil to produce beta diversity in Californian plant communities. *Ecology*, 94(9), 2007–2018.

Foody, G.M. (2011) Impacts of imperfect reference data on the apparent accuracy of species presence–absence models and their predictions. *Global Ecology and Biogeography*, 20, 498–508.

García, D. (2011) Efectos biológicos de la fragmentación de hábitats: nuevas aproximaciones para resolver un viejo problema. *Ecosistemas*, 20(2–3), 1–10.

Gonçalves, J., Alves, P., Pôças, I., Marcos, B., Sousa-Silva, R., Lomba, Â. et al. (2016) Exploring the spatiotemporal dynamics of habitat suitability to improve conservation management of a vulnerable plant species. *Biodiversity and Conservation*, 25(14), 2867–2888.

Grove, R., Evans Pim, J., Serrano, M., Cidrás, D., Viles, H. & Sanmartín, P. (2020) Pastoral stone enclosures as biological cultural heritage: Galician and Cornish examples of community conservation. *Land*, 9(1), 9.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T. et al. (2013). Predicting species distributions for conservation decisions. *Ecology Letters* 16(12), 1424–1435.

Hao, T., Elith, J., Lahoz-Monfort, J.J. & Guillera-Arroita, G. (2020) Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. *Ecography*, 43, 549–558.

Harrison, S.P. (2013) *Plant and Animal Endemism in the California Floristic Province*. Berkeley, CA: University of California Press.

Harrison, S.P. & Inouye, B.D. (2002) High β diversity in the flora of Californian serpentine "islands". *Biodiversity and Conservation*, 11(10), 1869–1876.

Honrado, J.P., Pereira, H.M. & Guisan, A. (2016) Fostering integration between biodiversity monitoring and modelling. *Journal of Applied Ecology*, 53(5), 1299–1304.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. et al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75, 3–35.

Izco Sevillano, J. & Rivas-Martínez, S. (2018) Pastos vivaces de los afloramientos ultrabásicos del NO de la Península Ibérica. *Acta Botanica Malacitana*, 42(2), 239–245.

Kaplan, G. & Avdan, U. (2017) Mapping and monitoring wetlands using sentinel-2 satellite imagery. *ISPRS Annals of Photogrammetry, Remote Sensing and Spatial. Information Sciences*, IV-4/W4, 271–277.

Kareiva, P. & Kareiva, I. (2017) Biodiversity hotspots and conservation priorities. In *Oxford Research Encyclopedia of Environmental Science*. Oxford: Oxford University Press.

Kruckeberg, A.R. (1984) *California Serpentines: Flora, Vegetation, Geology, Soils, and Management Problems*. Berkeley, CA: University of California Press.

Mandanici, E. & Bitelli, G. (2016) Preliminary comparison of Sentinel-2 and Landsat 8 imagery for a combined use. *Remote Sensing*, 8, 1014.

Marchese, C. (2015) Biodiversity hotspots: a shortcut for a more complicated concept. *Global Ecology and Conservation*, 3, 297–309.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, 15, 59–69.

Martimort, P., Arino, O., Berger, M., Biasutti, R., Carnicero, B., Del Bello, U. et al. (2007) Sentinel-2 optical high resolution mission for GMES operational services. In *2007 IEEE International Geoscience and Remote Sensing Symposium*. IEEE, pp. 2677–2680.

Marzialetti, F., Di Febbraro, M., Malavasi, M., Giulio, S., Acosta, A.T.R. & Carranza, M.L. (2020) Mapping coastal dune landscape through spectral Rao's Q temporal diversity. *Remote Sensing*, 12(14), 2315.

McFeeters, S.K. (1996) The use of the Normalized Difference Water Index (NDWI) in the delineation of open water features. *International Journal of Remote Sensing*, 17(7), 1425–1432.

Merritt, M., Maldaner, M. & de Almeida, A. (2019) What are biodiversity hotspots? *Frontiers for Young Minds*, 7, 29.

Moreno, J.C. (2008) *Red list of Spanish vascular flora*. Dirección General de Medio Natural y Política Forestal (Ministerio de Medio Ambiente, y Medio Rural y Medio Marino, y Sociedad Española de Biología de la Conservación de Plantas), Madrid.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.

Narayanan, J., Kothari, M., Pathak, S. & Jeyseelan, A.T. (2013) Assessing drought for arid regions using Satellite Derived Vegetation Index (MSAVI2) and TRMM data. *Indian Cartographer*, 32, 421–427.

Nieto Feliner, G. (1987) El género "Armeria" ("Plumbaginaceae") en la Península Ibérica: aclaraciones y novedades para una síntesis. *Anales Del Jardín Bótanico De Madrid*, 44, 319–348.

O'Connor, B., Secades, C., Penner, J., Sonnenschein, R., Skidmore, A., Burgess, N.D. et al. (2015) Earth observation as a tool for tracking progress towards the Aichi Biodiversity Targets. *Remote Sensing in Ecology and Conservation*, 1(1), 19–28.

Oberprieler, C., Greiner, R., Konowalik, K. & Vogt, R. (2014) The reticulate evolutionary history of the polyploid NW Iberian *Leucanthemum pluriflorum* clan (Compositae, Anthemideae) as inferred from nrDNA ETS sequence diversity and eco-climatological niche-modelling. *Molecular Phylogenetics and Evolution*, 70, 478–491.

Pardo, T., Rodríguez-Garrido, B., Saad, R.F., Soto-Vázquez, J.L., Loureiro-Viñas, M., Prieto-Fernández, Á. et al. (2018) Assessing the agromining potential of Mediterranean nickel-hyperaccumulating plant species at field-scale in ultramafic soils under humid-temperate climate. *Science of the Total Environment*, 630, 275–286.

Pérez-Silos, I., Álvarez-Martínez, J.M. & Barquín, J. (2019) Modelling riparian forest distribution and composition to entire river networks. *Applied Vegetation Science*, 22, 508–521.

Pham-Duc, B., Prigent, C. & Aires, F. (2017) Surface water monitoring within Cambodia and the Vietnamese Mekong delta over a year, with Sentinel-1 SAR observations. *Water*, 9(6), 366.

Regos, A., Gómez-Rodríguez, P., Arenas-Castro, S., Tapia, L., Vidal, M. & Domínguez, J. (2020) Model-assisted bird monitoring based on remotely sensed ecosystem functioning and atlas data. *Remote Sensing*, 12(16), 2549.

Regos, A., Vidal, M., Lorenzo, M. & Domínguez, J. (2020) Integrating intraseasonal grassland dynamics in cross-scale distribution modeling to support waterbird recovery plans. *Conservation Biology*, 34(2), 494–504.

Requena-Mullor, J.M., López, E., Castro, A.J., Cabello, J., Virgós, E., González-Miras, E. et al. (2014) Modeling spatial distribution of European badger in arid landscapes: an ecosystem functioning approach. *Landscape Ecology*, 29(5), 843–855.

Rivas-Martínez, S., Penas, Á., Díaz González, T.E., Cantó, P., del Río, S., Costa, J.C. et al. (2017). Biogeographic Units of the Iberian Peninsula and Baelaric Islands to District Level. A Concise Synopsis. In *The Vegetation of the Iberian Peninsula*, pp. 131–188.

Rodríguez, J.P., Brotons, L., Bustamante, J. & Seoane, J. (2007) The application of predictive modelling of species distribution to biodiversity conservation. *Diversity and Distributions*, 13(3), 243–251.

Rodríguez Oubiña, J. & Ortiz, S. (1991) Los pastizales pioneros vivaces de los suelos serpentínicos del NO ibérico. *Lazaroa*, 12(333), 344.

Santos, T. & Tellería, J.L. (2006) Pérdida y fragmentación del hábitat.pdf. *Ecosistemas*, 15, 3–12.

Schoener, T.W. (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51(3), 408–418.

Serrano, M., Carbajal, R., Ortiz, S., Iriondo, J.M. & Albert, M.J. (2009) Armeria merinoi (Bernis) Nieto Fel. and Silva Pando. In: Iriondo, J., Albert, M.J., Giménez Benavides, L., Domínguez Lozano, F. & Escudero, A. (Eds.) *Populations in Peril: Demographic Viability of Threatened Spanish Vascular Flora*. Madrid: Dirección General de Medio Natural y Política Forestal (Ministerio de Medio Ambiente, y Medio Rural y Medio Marino), pp. 69–72.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, 32(3), 369–373.

UNEP. (2010). Tenth Meeting of the Conference of the Parties to the Convention on Biological Diversity. 384.

Vanselow, K. & Samimi, C. (2014) Predictive mapping of dwarf shrub vegetation in an arid high mountain ecosystem using remote sensing and random forests. *Remote Sensing*, 6(7), 6709–6726.

Vila-Viçosa, C., Arenas-Castro, S., Marcos, B., Honrado, J., García, C., Vázquez, F.M. et al. (2020) Combining satellite remote sensing and climate data in species distribution models to improve the conservation of Iberian White Oaks (*Quercus* L.). *ISPRS International Journal of Geo-Information*, 9(12), 735.

Villero, D., Pla, M., Camps, D., Ruiz-Olmo, J. & Brotons, L. (2017) Integrating species distribution modelling into decision-making to inform conservation actions. *Biodiversity and Conservation*, 26(2), 251–271.

Wickham, H. (2016) *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer.

Wiegand, T., Naves, J., Garbulsky, M.F. & Fernández, N. (2008) Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. *Ecological Monographs*, 78(1), 87–103.

Yesou, H., Pottier, E., Mercier, G., Grizonnet, M., Haouet, S., Giros, A. et al. (2016) Synergy of Sentinel-1 and Sentinel-2 imagery for wetland monitoring information extraction from continuous flow of sentinel images applied to water bodies and vegetation mapping and monitoring. In *2016 IEEE International Geoscience and Remote Sensing Symposium (IGARSS)*. IEEE, pp. 162–165.

SUPPORTING INFORMATION

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

Appendix S1. Description of all spectral indices initially considered as candidate predictor variables, and the specificity and sensitivity values of the single-algorithm models across model replicates represented by species, algorithm and type of validation.

Appendix S2. Maps of the differences in the predicted habitat suitability of the three target species between 2018 and 2019.

How to cite this article: Ponce-Fontenla, S., Serrano, M., Carballal, R. & Regos, A. (2021) Sentinel 2 images enable reliable prediction of fine-scale habitat dynamics of narrow endemic plant species in serpentine soils. *Applied Vegetation Science*, 24, e12614. https://doi.org/10.1111/avsc.12614