

Distribution and conservation of the relict interaction between the butterfly *Agriades zullichi* and its larval foodplant (*Androsace vitaliana nevadensis*)

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Abstract Although Mediterranean mountains are considered biodiversity hot-spots, the presence of relict biotic interactions as a testimony of a past colder climate is an aspect frequently missed. Herein we investigate the distribution and conservation problems of a relict interaction in the Sierra Nevada mountains (southern Europe) between the butterfly *Agriades zullichi*—a rare and threatened butterfly—and its larval foodplant *Androsace vitaliana* subsp. *nevadensis*. We designed an intensive field survey to obtain a comprehensive presence dataset. This was used to calibrate species distribution models with absences taken at local and regional extents, analyze the potential distribution, evaluate the influence of environmental factors in different geographical contexts, and evaluate conservation threats for both organisms. We found 39 presence localities inhabited by the larval foodplant and the butterfly comprising 60.93 ha, with 82 % of the area concentrated in ten larger localities. The local and regional distribution models explained 68.7 and 85.0 % deviance, indicating a suitable area of 1,884.8 and 9,621.22 ha respectively. Topography and soil properties were the most important variables in the local model and temperature in the regional model. We observed several threats such as restricted extent of occurrence, lack of larval foodplant regeneration, the negative effect of the ski resort and a potential high sensitivity to climate

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change. Finally, we recommend some management measures in order to improve the conservation of key populations of both species, reinforcing *A. vitaliana nevadensis* populations and researching the importance of phenology in the persistence of this interaction under climate change.

Keywords *A. zullichi* · *A. vitaliana* subsp. *nevadensis* · Biotic interaction · Mediterranean mountains · Species distribution models · Random Forest

Introduction

Traditionally, the conservation literature has considered the Mediterranean mountains as biodiversity hotspots, rich in endemic and relict species of animal and plants (i.e. Blondel and Aronson 1999; Médail and Quézel 1999). The presence of relict biotic interactions on the high summits of such mountains is an interesting aspect frequently missed in the literature and also in conservation management. Such persistent relict interactions are the testimony of a colder climate that occurred during the glacial periods of the Quaternary, when the northern latitudes of Europe were covered by a massive ice sheet (Haubrich and Schmitt 2007). Under such acute environmental change, the periglacial areas were transformed into cold steppes, colonized later on by arctic-alpine species (Haubrich and Schmitt 2007; Schmitt and Haubrich 2008; Nieto-Feliner 2011). At the beginning of the last interglacial period the arctic-alpine species retracted polewards and upwards to colder areas, returning to its previous northern distributions or remaining isolated in the mountains of southern Europe (Hewitt 1996; Haubrich and Schmitt 2007; Schmitt and Haubrich 2008). However some of these species were not alone during their journey and certain interspecific relationships persisted. Some butterflies of the genus *Agriades* and their larval foodplants of the genus *Androsace* are a remarkable example of these interactions. *Agriades pyrenaicus* (Pyrenees, Cantabrian mountains and higher ranges between Balkans and Caucasus to Middle East), feeding on *Androsace villosa*, and *Agriades zullichi* (inhabiting the Sierra Nevada, southern Iberian peninsula), feeding on larval foodplant is *Androsace vitaliana* subsp. *nevadensis* (Munguira 1989; Dixon et al. 2009).

The main feature of interest of these relict interactions for conservation biologists is their isolation. Interacting species isolated in small-sized spots are very sensitive to stochastic environmental effects and natural fluctuations in its own population dynamics (Lesica and Allendorf 1995). A potential decrease in population size would eventually lead to genetic issues like inbreeding and genetic drift, opening the door to extinction. Furthermore, in a context of climate change research, the history of such species can help us to understand the ecological processes that climate warming is triggering. Isolated species in high mountains are actually in a very vulnerable situation under climate change, because they are still the fingerprint of past climate change. Currently most of these species have reached their upper elevation limits (Habel et al. 2010) and therefore they cannot migrate anywhere to evade warming, leaving them with only adaptation or extinction.

A relict butterfly and its relict larval foodplant

Agriades zullichi, considered one of the rarest and more threatened European butterflies, is a relict and endemic lycaenid butterfly inhabiting the Sierra Nevada (southern Iberian

peninsula). Since 1926, presence records of *A. zullichi* have been registered in 23 localities mainly situated on the north slope of the Sierra Nevada central area (Munguira 1989; Travesí and Pérez-López 2002; Travesí et al. 2008; Munguira et al. 2008; Van Swaay et al. 2010b). Considering its restricted range, *A. zullichi* has been classified as an Endangered species by IUCN. It has also recently been included in the category “Endangered of extinction” in the Endangered Species Act of Andalusia. *A. zullichi* is a monophagous species, being *A. vitaliana* subsp. *nevadensis* its unique larval foodplant, a relict and endemic plant of the Sierra Nevada which is known to be an allopatric subspecies of *A. vitaliana*. (Kress 1997; Dixon et al. 2009). *A. vitaliana nevadensis* is a perennial herbaceous plant with a cushion-like life form mainly pollinated by insects, and produces small seeds not adapted to long-distance dispersal (Dixon et al. 2009). *A. vitaliana nevadensis* has been reported to be highly sensitive to nitrification produced by cattle and *Capra pyrenaica* and no regeneration of populations has been observed (Blanca et al. 2002). Its conservation status is Vulnerable, according to the Andalusian Red List (Cabezudo et al. 2005). Both species (hereafter *Az-Avn*) can be found exclusively in the Sierra Nevada National Park (declared in 1999; 862.08 km²), inhabiting spots of acid soils rich in schists and quartz between the tree line and the high summits (maximum altitude at 3,482 m). The climate in such spots is determined by very cold winters, poor soils, intense solar radiation, long periods with snow cover and strong winds that can often reach more than 100 km/h in Winter (Anderson et al. 2011).

Despite the importance of both species given their biogeographical history and genetic exclusivity, today there is not enough information about their geographical distribution, the structure of their populations or the environmental factors influencing their distribution. Such knowledge is crucial to design conservation management strategies for both species. This study is aimed to fill the gaps of current knowledge about the spatial distribution and ecological requirements of *A. zullichi* and its larval foodplant, *A. vitaliana nevadensis*, with the objective to design the conservation measures needed to preserve such special coupled organisms. This knowledge and the management recommendations are also interpreted in a more global change context, taking into account possible effects of these components on the high Mediterranean mountain biota. This study was based on exhaustive field work intended to fulfill the following objectives: (1) update the information on the distribution of *Az-Avn*; (2) using the updated dataset to build a species distribution model for both species carried out at different geographical extents (local and regional); (3) evaluating the importance of different environmental variables and exploring the main conclusions in relation to conservation in a changing environment and, finally and as a conservation remark, (4) depending on the updated information provided, we make some recommendations to improve the adaptation skills of this ecological couple under a global change scenario.

Materials and methods

Field work

The starting point to obtain an up-to-date and reliable presence dataset of *Az-Avn* was a review of the available information on the distribution of both species in published literature and the official database on endangered flora of the Andalusia Government. Then, we designed an intensive field survey, both to confirm the presence of *A. zullichi* at the known populations of *A. vitaliana nevadensis*, and to find new co-occurrences of both species. To

do so, an expert in the distribution of *A. vitaliana nevadensis* (Ruíz-Girela pers. comm.) provided a map of known and also favorable areas that were prospected later on by seven people for 120 h per person, distributed over 23 days during the years 2011 and 2012. Each locality was visited during the central flying period of *A. zullochi* according to the phenology of the most accessible locations and our own experience. All the localities were visited under suitable conditions for adult butterfly activity (dry conditions, wind speed less than Beaufort scale 5, and temperature above 15 °C). The position of each individual of *A. vitaliana* subsp. *nevadensis* was established using a hand-held global positioning system (Garmin CS × 60; accurate to ±10 m). The presence of *A. zullochi* was checked following the guidelines of James et al. (2003): if two or more butterflies were seen in a patch one or more times, then a breeding colony was defined to be present. In each locality we invested a maximum of 2 h in order to confirm the butterfly presence. To compute the total area covered by *Az–Avn* we delimited the boundaries of each *A. vitaliana nevadensis* patch in which *A. zullochi* was observed by drawing the Minimum Convex Polygon on 95 % of the most external GPS landmarks (hereafter MCP95). Five percent of the larval foodplant presence records were excluded from the minimum convex polygon to prevent individuals appearing outside the main boundary (outliers). The estimated number of larval foodplant individuals, area, perimeter and average elevation of each locality were also recorded. All the geographical analysis was carried out with ArcGis[®] 9.3, with the help of Home Range Tools for the calculation of MCP95 boundaries.

Potential distribution

Presence records

We processed the GPS landmarks of *Az–Avn* to minimize pseudoreplication by ensuring a minimum distance of 20 m between adjacent points (Guisan and Zimmermann 2000), and obtained 600 presence records at 10 m resolution at which both species occurred simultaneously (Schweiger et al. 2012). We also generated two different sets of ‘zeros’ (absences and pseudo-absences) at two different geographical extents: ‘local’ and ‘regional’. The ‘local’ true-absences were intended to capture the differences in ecological variables between the presence records and the habitat immediately surrounding them (hypothetically, topography and soil properties, which are known to exert influence in plant distribution at local scales). To produce a comprehensive set of true-absences we combined three different sets of points: (1) absences obtained during the field work, defined one by one by the field technicians with GPS devices. (2) Absences extracted from GPS tracks: during the search for *A. vitaliana nevadensis* populations, the GPS devices automatically recorded the paths followed by the field technicians. We considered as true-absences the track segments without presence records of the plant. Finally, we transformed the tracks within the 100 and 1,000 m buffers around the plant populations into points to be used as absences in the SDMs. (3) Absences placed over high resolution aerial images (0.5 m, panchromatic and infrared) in a GIS environment, according to the field experience of the corresponding author and the field technicians. Absences represented raster cells of around 10 m resolution (same resolution of presence records) in which *Az–Avn* was not observed. We considered reliable this approach to define true-absences, since it was mostly based on ground truth information gathered actively and passively (GPS tracks) by the field technicians, while it also filled minor data gaps by considering the expert knowledge acquired during the field work.

Such absences (600 to balance the dataset prevalence) were selected within a buffer between 100 and 1,000 m away from the presence records of *Az-Avn*, following the guidelines of VanDerWal et al. (2009). The ‘regional’ pseudo-absence dataset was designed to represent the environmental conditions of the whole study area, with the purpose of capturing the influence of climate on the regional pattern of *Az-Avn* distribution. To do so we generated 10,000 points covering the Sierra Nevada National Park with the *randomPoints* function of the R package *dismo*, avoiding any overlapping with the presence records (Hijmans et al. 2012).

Environmental variables

To model the distribution of *Az-Avn* we focused on five conceptual groups of environmental variables selected to represent different direct and indirect gradients important to predict plant distributions (sensu Guisan and Zimmermann 2000): temperature, water availability, solar radiation, landcover and topography. In high mountains, temperature defines the upper limits of species distributions by imposing physiological constraints at different stages of the life cycle and influencing the thermoregulation of the butterflies (Bykova et al. 2012). To obtain seasonal and annual averages of temperature and rainfall at 10 m resolution we applied the climate mapping method proposed by Ninyerola et al. (2000), taking as input the daily records of 378 weather stations contained in the Information System of the Global Change Observatory of Sierra Nevada (<http://observatoriosierranevada.iecolab.es>). Solar radiation, which is especially intense in high mountains (Billings and Mooney 1968), is an essential resource gradient for plants because of its central role in photosynthesis, playing also an important role in butterflies thermoregulation (Ohsaki 1986; Vande Velde et al. 2011). We produced seasonal and annual maps with the averages of direct solar radiation and insolation time using the *r.sun* GRASS module (Suri and Hofierka 2004). During our field campaign we observed that *A. vitaliana nevadensis* inhabits locations with a very scarce vegetation cover, and a particular mineralogical composition that seems to be slightly different from the surrounding schists. To incorporate this factor into the model, we used the seven spectral bands of the Landsat 7 ETM+ sensor. In areas with a low vegetation cover, such bands allow to identify different kind of soils, since different soil types reflect radiation in different wavelengths due to differences in particle size and soil structure, moisture, the content in organic matter, the rate of carbonate mineral, or the proportion of quartz and iron oxides (Stoner and Baumgardner 1981). The correlation between spectral curves and soil composition has been established by different authors (Frazier and Cheng 1989; Demattê and Garcia 1999; Demattê and Nanni 2003). Furthermore, raw Landsat bands have been used before to model species distributions, because to use the original reflectance values improves the accuracy of predictions while avoiding the subjectivity loss of information that will arise from the selection of a classification method, the loss of data resulting from transforming a continuous variable into discrete classes, and misclassification errors (Shao and Wu 2008; Shirley et al. 2013). We used a Landsat scene (scene ES21; 25 m resolution for bands 1–6, and 12.5 m for band 7) taken from the Image 2000 project (image2000.jrc.ec.europa.eu). Image 2000 is the main source of data for updating the European Land Cover database (CORINE Land Cover). The Landsat scenes of Image 2000 are georeferenced and orthorectified, and therefore provide a high quality product for scientific research. Since it is well known that the Landsat bands in the visible spectrum (1, 2 and 3) are strongly correlated (Theseira et al. 2002), we computed the correlation among the seven Landsat bands, and found that there were three clusters of correlated bands above 0.5 Pearson

index: bands 1, 2 and 3; bands 4, 5 and 7; band 6. To retain as much information as possible without increasing the collinearity in the set of environmental variables, we used as predictive variables the first PCA component of bands 1, 2 3, the first component of bands 4, 5, 7, and the band 6. Both PCA components were correlated at -0.77 Pearson index, but we decided to retain both factors, since they represent very different wavelength intervals (0.45–0.69 vs. 0.77–2.35 μm). To represent vegetation cover we also computed the NDVI index according to Tucker (1979). This vegetation index represents primary productivity, and has been used successfully to calibrate species distribution models in other studies (Benito et al. 2013; Roura-Pascual et al. 2006). Despite the NDVI variable contains information from the bands 3 and 4, already used in both PCA components, it showed a low correlation with both variables (0.05 with the PCA of the bands 1, 2 and 3, and -0.40 with the PCA of the bands 4, 5 and 7).

Finally, to represent ecological gradients not yet considered in the variables described before, we derived a set of topographic descriptors: slope, topographic position (difference in elevation between a cell and surrounding cells within a 200 m radius; Guisan et al. 1999) and topographic complexity (diversity of slope, aspect and elevation values within 200 m; Jetz et al. 2005). To reduce multicollinearity, we applied the Variance Inflation Factor method (VIF, R library HH; Heiberger 2012). Each conceptual group of environmental factors used to model the distribution of *Az-Avn* was finally composed of: water (mean annual rainfall), temperature (annual average, summer average and winter average), land cover (NDVI and the two PCA components of the Landsat bands), topography (topographic complexity and topographic position) and solar radiation (annual average of direct solar radiation).

Species distribution modeling

It is well known that different modeling algorithms provide results of different reliability (Elith et al. 2006). We searched for the most suitable algorithm to model the occurrence of *Az-Avn* by evaluating the results of eight different methods (see Table 1). Each algorithm was evaluated thirty times on each dataset ('regional' and 'local') computing AUC (Fielding and Bell, 1997) by applying random data splitting without replacement, using 100 presences and 100 absences to evaluate on each iteration. The most suitable algorithm in this previous trial was Random Forest, which was then used to model the distribution of *Az-Avn* at both geographical extents.

Random Forest is an ensemble classifier based on decision trees that was designed to fit complex and nonlinear surfaces from high-dimensional input data (Breiman 2001; Cutler et al. 2007). The algorithm uses bootstrap aggregating ("bagging") to generate subsets of cases and predictors. Each subset is used to define a single regression tree, and the process is repeated until the total number of trees is reached (500 by default). The final prediction for a single case is the mode vote for that case across all the trees of the Random Forest algorithm.

During our initial trials with the R library 'randomForest' (Liaw and Wiener 2002) we observed that the selection of different absences or pseudo-absences on different runs produced slightly different results. To deal with this variability, we generated 100 models for each geographical extent changing the absences used to calibrate the model at each run. We used data-splitting without replacement to select 500 presences and 500 absences to calibrate each model, and 100 presences and 100 absences to evaluate. Each model was evaluated using the AUC scores provided by the 'evaluate' function of the R package 'dismo', and the

Table 1 Modeling algorithms

Algorithm	Acronym	Software	Reference
Boosted regression trees	brt	R package Dismo	Hijmans et al. (2012)
Maximum entropy	max	MaxEnt	Phillips et al. (2006)
Artificial neural networks	ann	R package nnet	Venables and Ripley (2002)
Random Forests	rfo	R package randomForest	Liaw and Wiener (2002)
Support vector machines	svm	R package kernlab	Karatzoglou et al. (2004)
Logistic regression	log	R core	R Development Core Team (2012)
Generalized additive models	gam	R package gam	Hastie (2011)
Multivariate adaptive regression splines	mar	R package earth	Milborrow (2012)

explained deviance computed by the function ‘randomForest’. To obtain comparable AUC scores, the models were evaluated using the absences of the ‘local’ dataset.

We analyzed the importance of predictive variables and the response curves for each model in order to obtain a better understanding of the distribution of *A. zulichii* and *A. vitaliana nevadensis*. Random Forest measures variable importance computing the Increment in Node Purity (IncNodePurity), which is the total decrease of residual sum of squares when splitting a decision tree on the target variable averaged across all the Random Forest trees. We computed the average of increment in node purity across the 100 models to analyze which were the environmental variables influencing the distribution of *Az-Avn* at each geographical extent. To obtain reliable response curves describing the habitat requirements of the species, we used the function ‘partialPlot’, which computes and plot the marginal effect of each variable on the model response. To account for the variability induced by the different absences and pseudo-absences in the response curves, we summarized the 100 response curves for each variable across the 100 models by computing a single Generalized Additive Models (GAM) for each group of response curves with the R library ‘gam’ (Hastie 2011).

Finally we averaged the spatial projections of the 100 models of each spatial extent (Marmion et al. 2009), and applied as a threshold the average of the maximized sum of true positive and true negative rate (Liu et al. 2005) rate across the 100 models of each geographic extent. Such thresholds were computed using as reference the absences of the ‘local’ dataset, because it resembles better the concept of “real absences”, and it is preferable to define a threshold with biological significance. We used both binary maps to compare the local and regional models, and to compute the area and the number of patches of the suitable habitat for *Az-Avn*.

Results

A total number of 39 localities of *Az-Avn* were located during the field work (Fig. 1) on an altitudinal band comprised between 2,405 and 3,057 m.a.s.l. Such colonies covered a surface area of 60.93 ha with an average perimeter of 0.44 km. A total of 4,615 individuals of *A. vitaliana nevadensis* were counted in these localities.

The Fig. 2 shows the results of the model evaluation involving eight algorithms calibrated with absences (local model) and pseudoabsences (regional model). The final local and regional models showed a very good discriminative power according to its AUC values

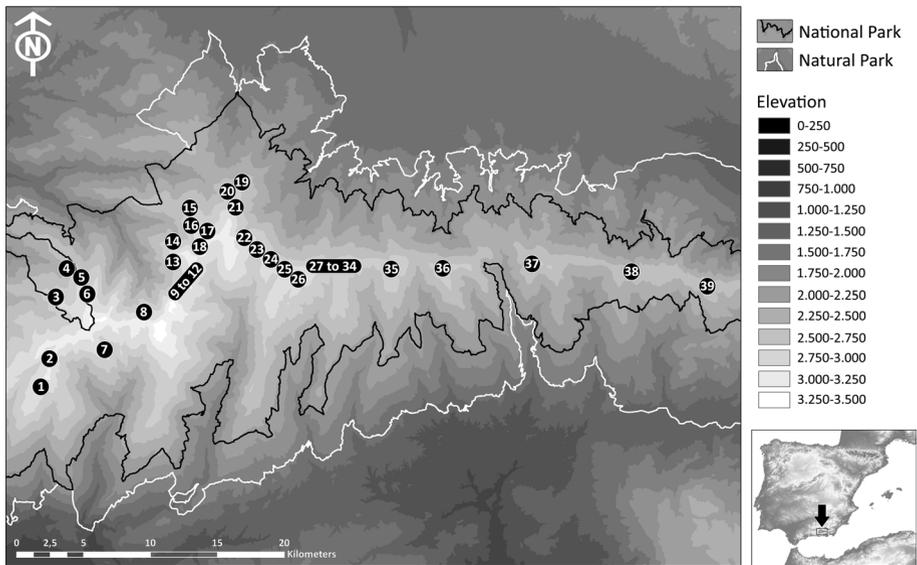


Fig. 1 Map of the study area (Sierra Nevada National Park) showing the distribution of the subpopulations of *A. zulichi-A. vitaliana nevadensis*. Subpopulations 16, 17, 19, 21, 22, 28, 30, 33, 35 and 39 hold the 82 % of the species distribution

(AUC local = 0.967; AUC regional = 0.930) and high values of explained deviance (local = 68.729 %; regional = 85.020 %). Resulting habitat suitability thresholds to convert each continuous model into a binary surface were 0.66 for the local model and 0.55 for the regional model. The surface area of suitable habitat defined by the local model was 1,884.88 ha arranged in 2,525 patches. In the regional model the surface area was 9,621.22 ha arranged in 1,869 patches (Fig. 3).

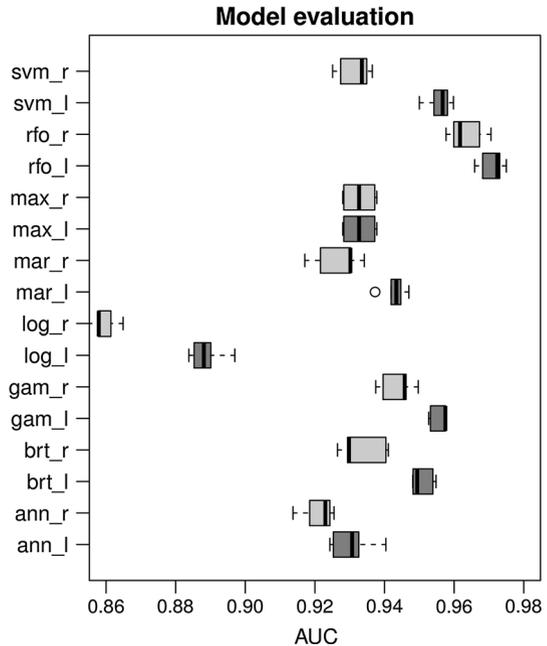
The most important variables in the ‘local’ model were topographic position, PCA of Landsat bands 1, 2 and 3, and NDVI (see Fig. 4). For the ‘regional’ model the most important ones were average annual and winter temperatures, followed by the maximum summer temperatures and the NDVI. The response curves for both models were consistent (and completely equivalent), showing the inflexion points at the same values, thus offering easily interpretable information about the habitat requirements of *Az-Avn* (Fig. 5). According to such curves, the suitable habitat of *Az-Avn* showed the following ecological characteristics: (1) a topographic position higher than zero, which is representative of ridges or elevated spots; (2) very low values of NDVI, indicative of very scarce vegetation cover; (3) a solar radiation between 4,000 and 6,000 Wh/(m²)/day; (4) a mean annual temperature between 6 and 10 °C; (5) a mean winter temperature between −3 and −6 °C; (6) a mean summer temperature between 23 and 27 °C.

Discussion

Observed distribution

Our results represent a complete, up-to-date snapshot of the barely known distribution of one of the most imperiled butterfly species in Europe and its larval foodplant (Van Swaay et al.

Fig. 2 Boxplot of the AUC results for the 30 runs of each algorithm at both geographical contexts (r = regional; l = local). AUC is a measure of the discriminative power of a model, and represents the probability to obtain a higher suitability value for a presence record selected by chance when compared with an absence record selected by chance. Abbreviations: *svm* support vector machines, *rfo* Random Forest, *max* maxent, *mar* multi adaptive regression splines (MARS), *log* logistic regression, *gam* generalized additive models, *brt* boosted regression trees, *ann* artificial neural networks



2010a). Our work is based on a well designed field survey and the most robust modeling methods currently available. The results of this work provide a comprehensive knowledge on the distribution of *Az-Avn* and a complete and intuitive description of its habitat requirements. Our results are highly important for designing management strategies aimed at improving the conservation status of these threatened species. Furthermore, our results would also be of great interest to conservation practitioners and biogeographers working with relict, endemic and vulnerable species in mountainous environments, considering that the information on alpine and sub-alpine endemic species is in general very scarce (Settele and Kühn 2009).

We have found 39 localities of *Az-Avn* located near the summits of the Sierra Nevada, covering a surface area of 60.93 ha. This implies a low number of localities with a very restricted extent of occurrence. The structure of *Az-Avn* localities consists of a set of more extensive patches in the central area of the Sierra Nevada and several isolated and small patches at the periphery (see Fig. 1). We have also observed a few isolated localities of *A. vitaliana nevadensis* without individuals of *A. zullichi*, but taking into account that butterfly populations rarely persist for large time periods in small and isolated patches (Thomas 1992), this situation may be common.

Potential distribution and environmental predictors

In this paper, we have developed a robust model using the Random Forest algorithm to represent the distribution of an endangered, endemic and relict butterfly and its larval foodplant. The strength of our model relies on several key points: (1) the availability of high quality presence data obtained from a comprehensive field survey; (2) an ecologically sounding selection process of the environmental variables; (3) a screening process to select the most suitable modeling algorithm; (4) an honest approach used to deal with the uncertainty induced by the selection of different groups of absences and pseudo-absences in the model evaluation and measuring the variable importance; (5) an effort to study how

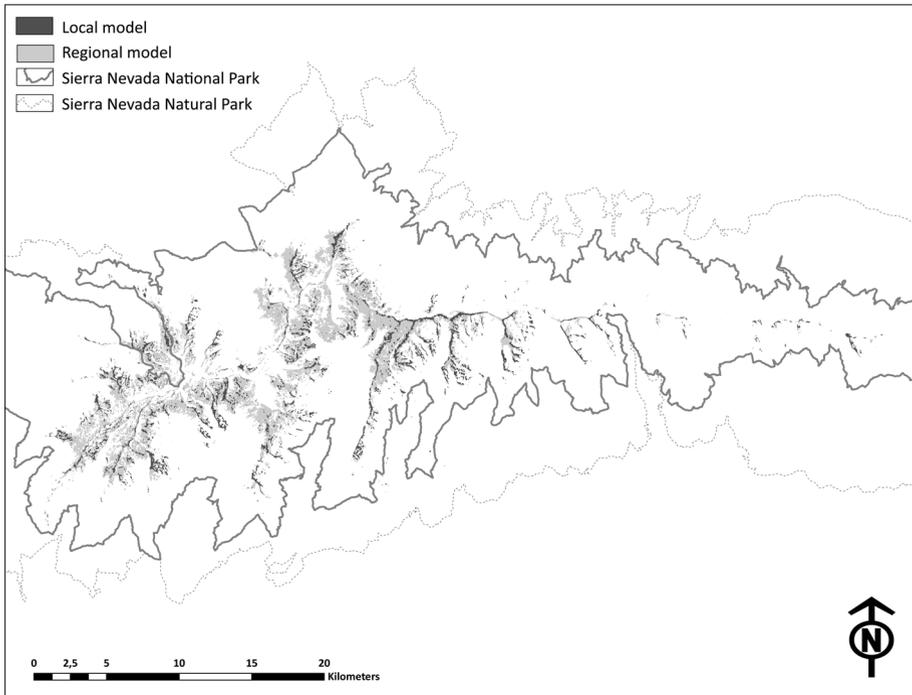


Fig. 3 Local (dark grey) and regional (light grey) distribution models of *A. zullichi*–*A. vitaliana nevadensis*

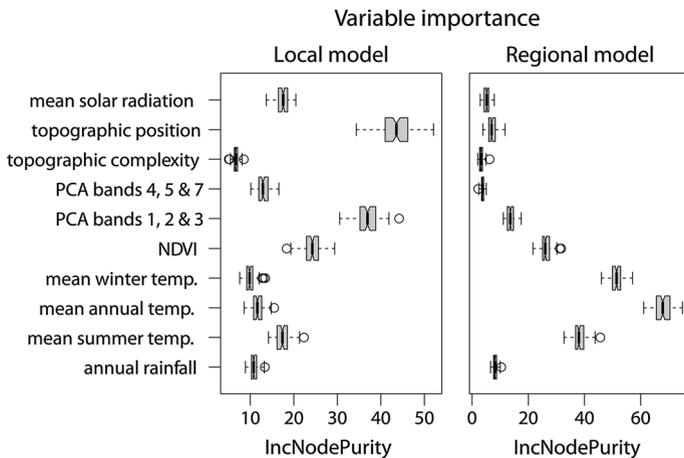


Fig. 4 Relative importance of predictor variables in the distribution of *A. zullichi*–*A. vitaliana nevadensis*. The variable importance was measured as ‘increase in node purity’, a standard procedure when modelling with Random Forest. ‘Node purity’ represents how well the model fits when the target variable is selected to be the first node in a regression tree, averaged over all the regression trees generated with such variable

the extent of the absences and pseudo-absences at different geographical extents (‘local’ and ‘regional’) affects model outcomes, and how can we interpret such results in a biologically meaningful way.

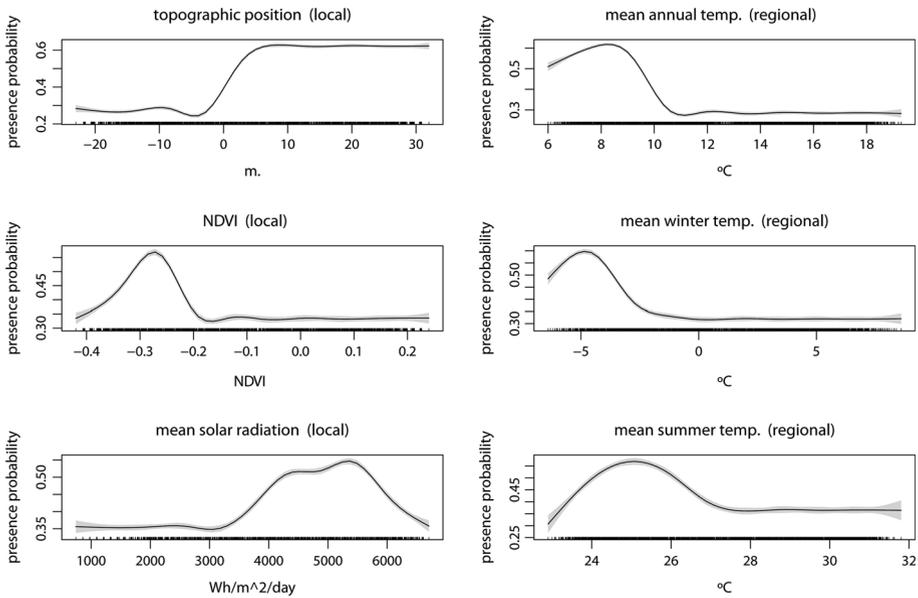


Fig. 5 Response curves: the panel represents the response curves of the four climatic variables according the local (*left*) and regional models (*right*) that were found to be the most important to explain the distribution of *A. zullochi*–*A. vitaliana nevadensis*

We have calibrated two different models for the same species by selecting absences and pseudo-absences covering different geographic extents (‘local’ and ‘regional’). The idea that different geographical extents in the absence dataset affect model outcomes is not new, and has been comprehensively tested by VanDerWal et al. (2009). These authors found that Random Forest models calibrated with absences from large extents provide good regional discrimination, but were unable to reproduce the finer patterns of species distribution. This procedure led to inaccurate results that were not acceptable, as the main goal of a model was to be used for conservation purposes. VanDerWal et al. (2009) have also found that variable importance changes along with the geographical extent of the pseudo-absences, as we did, but we don’t see that either as a problem or as the effect of a statistical artifact, but as a result of how absences and pseudo-absences are defined at different geographical extents are able to capture the “hierarchy of factors operating at different scales” (sensu Pearson and Dawson 2003). According to the modeling framework proposed by Pearson and Dawson (2003), different environmental variables have influence on species distribution at different geographical scales. For example (see Fig. 5 in Pearson and Dawson 2003) climate (represented by temperature and water in this study) imposes physiological restrictions to species presence from global to regional scales (10,000–200 km), whereas land-use and soil type (landcover) exert their influence from landscape to site scales (200 km–10 m). Despite the fact that we have grouped the environmental variables in different conceptual pools than those proposed by Pearson and Dawson (2003), this hierarchy of factors is perfectly represented in our results. They show that temperature plays a key role defining the distribution according to the ‘regional’ model, whereas land cover and topography are the main drivers of the distribution at ‘local’ scale. The high importance of temperature in the ‘regional’ model is not surprising,

considering that the different subspecies of *A. vitaliana* can be found in most of the European mountain ranges at elevations between 1,500 and 3,300 m (Dixon et al. 2009). According to Boucher et al. (2012), the adaptation of the *Androsace* species to cold would probably have come from an ancestor adapted to inhabit cold steppes, which later on was isolated during the elevation of the Alpine belt. This isolation apparently enhanced the selective pressures towards cold tolerance, promoting the appearing of the cushion life form, which elevates the temperature inside the plant and allows the organism to survive under the snow pack (Larcher et al. 2010). The cushion structure of *A. vitaliana* subsp. *nevadensis* is supposed to increase the survival probability of *A. zullichi* caterpillars during the winter. According to the local model, topographic position was the most important variable, showing an evident threshold at 0, which implies that *A. vitaliana* require elevated spots in relation to its surrounding area. The following variables in order of importance were the first PCA component of the Landsat bands 1, 2 and 3, and the lower values of NDVI. Considering that low NDVI values indicates a scarce vegetation cover, or even bare ground, and that under such conditions the Landsat ETM+ sensor mainly captures soil reflectance. Bands 1, 2 and 3 (0.45–0.69 μm wavelength: red, green and blue in the visible spectrum) are useful to discriminate vegetation types, vegetation vigor, and changes in vegetation structure when reflectance is low. According to the “Spectral Characteristics Viewer” provided by the USGS (http://landsat.usgs.gov/tools_spectralViewer.php), the mineral chlorite can be easily identified when there are slightly higher reflectance values in the same wavelength, as those in which *Az-Avn* presence records were found. Chlorite is a very conspicuous mineral in multispectral analyses (Hewson et al. 2001; Ji et al. 2006), and a main component of the metamorphic schists of Sierra Nevada (Martín-García et al. 1998; Sánchez-Marañón et al. 1999). Therefore, we hypothesize that the intermediate values of the PCA component of the Landsat bands 1, 2 and 3 represents a key soil characteristic, probably a change in the content of chlorite, that according to our model, is relevant for the distribution of *Az-Avn* at the local scale. This hypothesis is in agreement with our field observations, because the soil composition at the *Az-Avn* localities apparently showed a higher proportion of quartz than the surrounding environment, that is dominated by schists rich in chlorite. The importance of a proxy of soil composition in our model is in agreement with the findings of Alvarez et al. (2009), which revealed the importance of substrate and soil properties as one of the main drivers of alpine species distributions.

In our models we have not considered the human effect over the presence of *Az-Avn*, because it inhabits high summits far away from human settlements. But after a thorough analysis of the ‘local’ model, the known distribution of *Az-Avn*, and the area covered by the Sierra Nevada ski resort, we can conclude that there are some areas in the ski station that resemble the habitat requirements for *Az-Avn*, which have been visited during the field work, but did not contain populations of *Az-Avn*. This finding shows how the ski resort, despite its limited surface area when compared with the whole area of the National Park, exerts an impact over the distribution of *Az-Avn*. This situation has been previously reported in other mountainous habitats like the Swiss Alps (Wipf et al. 2005). Munguira et al. (2008) also reported serious damage to the habitat of one population due to urban development and the construction of a road for a ski championship in 1997. Apart from this, it is worth noting that the ski resort is placed in one of the margins of the distribution of the butterfly and its larval foodplant, this fact would be less threatening than if the location was in the centre of the distribution area, where its impact would be much higher.

Threats over *A. zullichii* and *A. vitaliana*

According to Stefanescu et al. (2011), the main threat to specialist species inhabiting mountainous habitats is global warming combined with habitat loss caused by anthropic activities. During our work with *Az-Avn* we have observed several of these threats that have the potential to compromise the persistence of both the larval foodplant and the butterfly. Regarding the larval foodplant, it is an endemic and rare plant that presents a cushion like form, which is a typical adaptation to cold environments. This adaptation to a cold, high mountain climate is clearly shown in our 'regional' model, which emphasizes the selection of mean winter, summer and annual temperatures. This endemic plant also has a narrow and highly fragmented distribution, inhabiting spots with very restrictive habitat requirements that, according to our 'local' model, are very scarce in the Sierra Nevada. The combination of restrictive habitat requirements with a low tolerance to the nitrification produced by cattle and the complete lack of regeneration evidence (Blanca et al. 2002) has probably resulted in an overall low number of individuals (~1,000 according to Blanca et al. 2002, but at least 4,615 according to our field data). Regarding the butterfly, its populations are mainly concentrated in a few patches of *A. vitaliana nevadensis*, (82 % of the global distribution of the species in just 10 big patches in the central Sierra Nevada range), increasing its vulnerability to stochastic environmental effects. Considering the information presented above, it can be assumed that both species are of conservation concern, but now we are going to put such facts into the context of global change. The consequences of climate warming to the distribution of butterflies inhabiting Mediterranean mountains have already been reported by Wilson et al. (2007) in the Sierra de Guadarrama (central Spain), where the lower altitudinal limit of distribution of 16 butterfly species has shifted upwards 212 m (\pm SE 60) in a 30 years period with an average temperature increase of 1.3 °C. Climate change is also increasing plant diversity at summits of Mediterranean mountains because plants inhabiting vegetation belts at lower elevations are shifting upwards, imposing new competitive constraints to the plants already inhabiting the high summits (Gottfried et al. 2012; Pauli et al. 2012). Such consequences are expected to worsen for both species in the Sierra Nevada according to the climatic simulations performed by Benito et al. (2011). This study forecasts an increase in mean annual temperature between 2.3 and 7.0 °C for the end of the century and an isotherm shift rate of between 5 and 10 m per year. Consequently the predicted temperature rise in the Sierra Nevada will have the potential to disturb the potential habitat of *Az-Avn*, either shifting its lower altitudinal distribution limit and reducing the available potential habitat to the higher summits (the availability of habitat above the present distribution of *Az-Avn* is still very limited), or increasing the likelihood of colonization events by new plant and butterfly species inhabiting lower elevations, that would probably intensify interspecific competition. In addition, butterflies are poikilothermic organisms, and temperature partially controls its phenology and behavioral patterns (Roy and Sparks 2000). According to our analyses, *Az-Avn* requires a very narrow range of optimum temperatures to develop its life cycle (optimum mean summer temperature between 24 and 26 °C), and therefore, even a small increase in temperature at the high summits has the potential to disturb the butterfly's life cycle.

Indeed, butterflies inhabiting high elevations have a short window of opportunity to complete their mating and egg-laying (cold hampers the ability to fly), and slows down egg maturation (Illán et al. 2012). Under this scenario the future for *A. zullichii*, *A. vitaliana nevadensis* and any other glacial relict species inhabiting high summits must be of concern (Merrill et al. 2008).

Conservation status, guidelines for management, and future research

Given the current conservation status of *A. zullichii*, the lack of regeneration evidence for *A. vitaliana nevadensis*, and the potential threats due to climate change that would affect them in the near future, we think that the legal protection provided by the status of the Sierra Nevada as a National Park may not be enough to guarantee the conservation of *Az-Avn*, and some management measures are needed in order to improve the adaptation skills of this ecological couple in a global change scenario. To ensure the conservation of this ecological interaction we propose some management guidelines in the short-term based on the results of this study. We also suggest new research lines to fill the gaps in our current knowledge about the ecology of both species, necessary for formulating further management recommendations:

Firstly, it is crucial to obtain a precise delimitation of every locality of *Az-Avn*. Despite the fact that our field survey was intended to be as comprehensive as possible, probably some undiscovered localities remain. Our 'local' model should help us to design a complementary survey to explore suitable spots not yet visited (Guisan et al. 2006). Secondly, and following the guidelines of Munguira et al. (2008) about the conservation of *A. zullichii*, we recommend to design and implement a reserve to protect a network of key localities, restricting tourist access and limiting the presence of livestock. Finally, the most important measure should be to reinforce the localities of *A. vitaliana nevadensis* in order to compensate the lack of regeneration of the natural populations and to improve the larval resource density. This task would be especially critical in the main localities because of their expected importance in the maintenance of peripheral nuclei.

Since there are still a lot of unanswered questions about the ecological processes involved in the persistence of *Az-Avn*, it is crucial to develop several research lines in order to provide an effective conservation plan in the long term. Firstly, a study of the abundance of *A. zullichii*, patch quality and overall connectivity of *A. vitaliana nevadensis* patches is essential to know how this metapopulation works and to elucidate the role of smaller and isolated populations, where probability of extinction is expected to be higher (Foose et al. 1995; Hovestadt et al. 2010). Secondly, it would be particularly important to analyze the drivers of phenology of both species, and searching for potential phenological mismatches under climate change scenarios, that would eventually disrupt the interaction between the two organisms (Singer and Parmesan 2010). Finally, it is also important to implement experiments at a microhabitat scale, to know the effects of temperature variations, moisture or snow cover permanence on plant conditions and on different butterfly stages.

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