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REVIEW ARTICLE

Species Distribution Modeling - a conservation tool with a wide spectrum of applications in Central Asia

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ABSTRACT

The goal of this paper was to review and illustrate the utility of SDM for solving conservation problems. Using real-world examples, I show a variety of uses for SDM, and then review the existing and potential applications of SDM for plant conservation in Central Asia. Central Asia is the region with a high number of endemic species that have narrow habitat specialization and very restricted ranges. Many of these species are red-listed and known from only a few or a single location. Any plans for their recovery must be based on the estimates of their area of occupancy and critical habitat, as well as the knowledge of their habitat requirements and potential range. SDM can be used for obtaining this information. The predicted ranges then can be used for species translocations, identification of biodiversity and endemism hotspots and reserve design.

Key words: conservation planning; reserve design, reintroduction, restoration; threatened species

What is SDM

Species distribution modeling (SDM) is a rapidly developing discipline that associates, using sophisticated statistical tools, georeferenced observations of species occurrence with multiple environmental predictors. A model estimated from observations can then be applied to produce digital maps of spatial prediction of the response variable, for example, probability of species occurrence or habitat suitability under past, current or possible future conditions. This discipline has resulted from, on one hand, the growing need to handle and analyze the spatial distribution of biodiversity, and on the other hand, the emergence of GIS tools addressing this need. The instantly growing popularity of SDM is due to the steadily increasing reliability of SDM predictions and the availability of global biodiversity and environmental datasets.

Maps of actual or potential species distributions or habitat suitability, produced using statistical and related methods, are essential for many aspects of environmental and conservation research and planning. The procedures for the development of these predicted maps are collectively known as species distribution modeling (SDM). Alternative names are environmental, bioclimatic, or species niche modeling and habitat suitability modeling. In the past two decades, we have been witnessing, on the one hand, a boom in the development of SDM as a discipline and the proliferation of its methods, and on the other hand, an instantly growing interest in SDM from the conservation practitioners and the availability of user-friendly SDM software. A review of the use of SDM by Guillera-Arroita et al. (2015) revealed

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a broad range of SDM applications: for managing endangered species (16% of papers), controlling threatening processes (8%), predicting the impacts of climate change (13%), understanding phylogeographic patterns (9%) and managing landscapes (8%) and biological invasions (7%).

Any SDM has one of the following goals: to estimate the species' environmental niche; to evaluate the relative suitability of the habitat either currently occupied by the study species or lacking species occurrence records, or to assess changes in the suitability of habitat over time under a specific environmental change scenario (Warren & Seifert 2011). If a study focuses on species niche parameters, then SDM results will provide insight into species environmental tolerances or habitat preferences (i.e. will identify the most important environmental or biotic factors directly affecting a species, as well as the range of these factors' values or categories within which a species can have viable populations. However, if the study aim is different, the outcome will be maps of suitable habitat. It is often of little interest for conservation practitioners which of the many interrelated and highly co-varying factors determine the suitable species range. In many conservation projects, it is more important to have the exact locations of suitable for a species habitat.

Any SDM procedure has three parts: the ecological, data, and statistical models (Austin 2002). The ecological model is formulated using a relevant ecological theory that conceptually links environmental predictors and species distribution data through a response function. In simple words, it's a model of what abiotic and biotic factors, at what scale and how, control species distributions in space. This model will be used or tested in SDM. A data model consists of decisions made regarding how data for modeling are collected, measured, or estimated. A statistical model includes a choice of modeling methods and statistical tests for model fitting and evaluation.

To implement predictive mapping, the following SDM elements should be available: data on species occurrences in geographical space (always species presences and species absences if available); digital maps of environmental variables that are believed to influence habitat suitability and therefore species distribution; a quantitative or rule-based model linking species occurrence to environmental predictors and methods for evaluating the validity of predictions; and a geographic information system (GIS) for producing maps of predicted species occurrence or habitat suitability from the model output. The listed above goals of SDM can be classified as requiring either interpolative or extrapolative forecasting, that is, whether the goal is filling the gaps in an under-surveyed species range or predictions that go beyond the currently known species range in space and time. These two general uses of a produced species distribution model, with a list of possible conservation applications, are shown in Fig. 1.

The SDM procedure as it evolved from a simple single species projection to complicated, often multi-species and using additional data algorithms, can be divided into three parts (Di Cola et al. 2017) (Fig. 1). Core modeling (or processing) analyses quantify species-environment relationship and make spatial predictions both at the individual species and community levels. This is an essential part of any SDM. The other two parts are needed to improve SDM performance or get additional insights beside those provided by core modeling analyses. Pre-modeling (or pre-processing) analyses are performed on the observational data alone (e.g. filtering of occurrences, variable selection, calculation of phylogenetic diversity or species co-occurrence measures). Finally, post-modeling (or post-processing) analyses use the model predictions, but incorporate additional data such as biotic interactions or dispersal capabilities.

Ecological theory

The niche concept is fundamental to SDM because it emphasizes species requirements, first of all in terms of (multiple) causal abiotic

factors that control the distribution of species. The classic definition of a niche given by Hutchinson (1978) is "… the hypervolume defined by the environmental dimensions within which that species can survive and reproduce". However, in niche considerations it is important to keep in mind that the viability of a population (that is, the ability to survive and reproduce) can vary substantially across the species range (Pulliam 2000). Some populations (with a positive growth rate) can serve as "sources" for "sink" populations having a negative growth rate (Pulliam 1988).

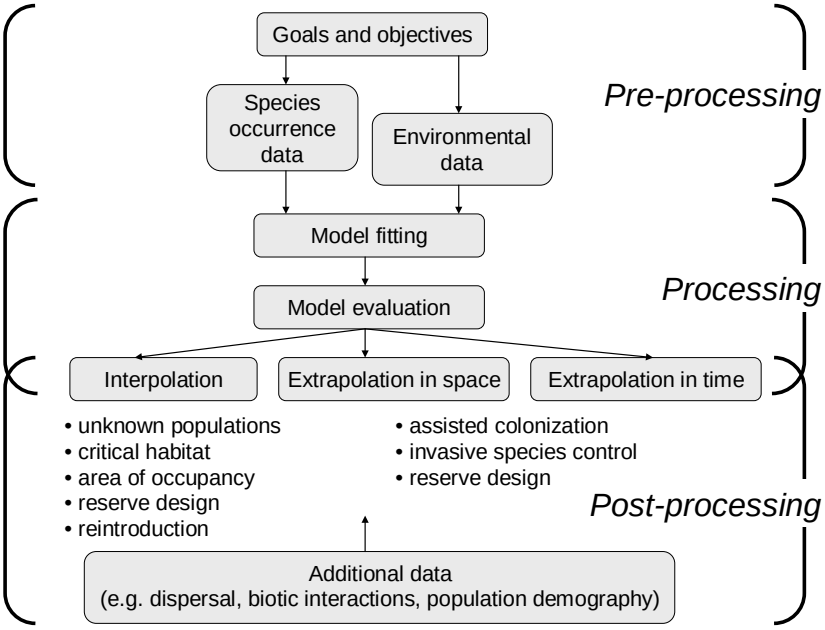

Fig. 1. SDM framework in the conservation context. Two general uses of the produced model (interpolative and extrapolative forecasting) are shown with a list of possible applications.

On the other hand, patches of suitable habitat can be surrounded by a hostile matrix, and while some of these patches may be inhabited, others may not, and the species absence from a patch can either a result of local extinction or because of dispersal limitations (Hanski 1999). In other words, a species can be found in unsuitable (sink) habitat, or it may not be present in a suitable habitat. It would be correct to refer to a species niche talking about the extant populations which growth rate is positive, or currently unoccupied locations able to support a positive population growth rate, but not about sinks or locations where populations went extinct. These considerations, that stem from metapopulation theory (Hanski 1999) and source-sink theory (Pulliam 1988), should supplement the classic niche concept of Hutchinson (1978) as an ecological framework for explaining the relationship between species distribution and suitable habitat. Since most SDM studies deal with species occurrence data and almost never with fitness data, it should be clear that habitat occupancy is not equivalent to habitat suitability, and is only a rough approximation of the latter.

An important aspect of modern niche concepts is the distinction between fundamental and realized niche. According to Hutchinson (Hutchinson 1957, 1978), the *fundamental niche* of a species comprises a subset of the environmental space, constrained by combinations of variables that allow survival and reproduction of individuals, while the *realized niche* is the actual niche space occupied by the species and is a subset of the fundamental niche constrained by biotic factors (competition, predation). Refinement to this

concept based on metapopulation and source-sink theories applied in geographical space (Fig. 2) shows that the realized niche (i.e. the currently occupied environmental space) is not necessarily a subset of the fundamental niche, e.g., in the case of "sink" habitat or dispersal limitation. In Fig. 2, based on Soberon (2007), area A is a geographic area with an appropriate set of abiotic factors for the species (corresponding to the fundamental niche); B is the area where the right combination of interacting species occurs; and M is the area accessible to the species within a given time frame, given its dispersal capacities. A realized niche in geographical space that does not account for dispersal limitations would be A ∩ B, but in fact the true realized niche, equivalent to the current geographic distribution of the species, is A ∩ B ∩ M.

This scheme has interesting implications. First, it suggests that the extent of study area should cover areas of species potential distribution; the latter, in certain cases, may extend far beyond the current species range. Second, if we want to generate a map of species potential distribution, i.e. environmentally suitable locations in which a species can occur according to its environmental tolerances, we need to use the presence data only. By not incorporating absence data from climatically suitable localities, we will be able to identify a potential species range including areas currently unoccupied due to historical events, biotic interactions or dispersal limitations.

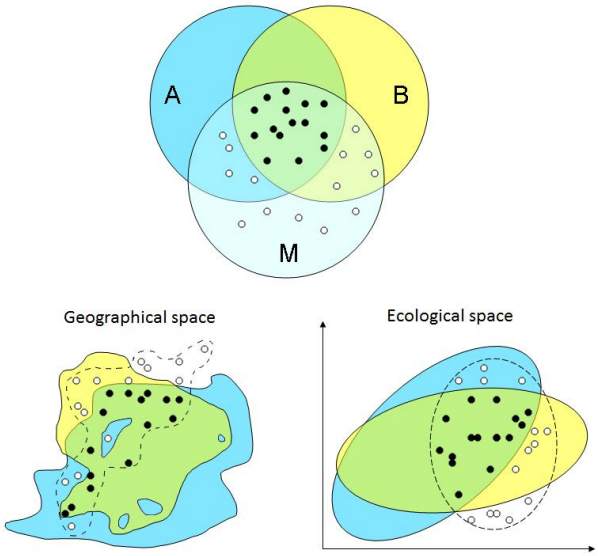

Fig. 2. A niche concept (modified from Soberon 2007) visualized in geographical and ecological space. A and B are the geographic areas where the abiotic factors (A) and biotic factors (B) would allow the intrinsic population growth rate to be positive; M is the geographic area that is accessible to a species within a given time frame, given its dispersal capacities. Solid circles represent the source populations having a positive growth rate and open circles denote sink populations with negative growth rate. Note the green area having the optimal combination of abiotic and biotic conditions that is currently not occupied due to dispersal limitations. Without considering dispersal limitations and population dynamics the area delimited by a broken line would be regarded as the realized species niche.

It is advisable, before doing SDM, to think about how the results will be interpreted in terms of the species niche concept. There is no agreement among those using SDM in their research as to what is actually modeled in SDM, the fundamental species niche, the realized niche, or just the probability for a location to be occupied. Some (e.g. Soberon &

Peterson 2005) argue that SDMs (at least those based on coarse-scale climate variables (bioclimatic niche modeling) describe the species fundamental niche. Others (e.g. Austin 2002) consider the outcome of SDM to be the realized niche, since the observed species' spatial distributions that are used in SDM, are constrained by non-climatic, including biotic, factors. On the other hand, when this realized niche, described by a statistical model, is mapped in geographical space, it depicts a potential distribution that differs from the actual distribution because it does not account for dispersal limitations (Guisan & Thuiller 2005; Araujo & Guisan 2006; Soberon 2007). Many simply prefer to avoid the term "niche" and use instead the term "distribution model" both for the model itself and its output mapped (e.g. Kearney 2006; Jiménez-Valverde et al. 2008; Franklin 2009).

Application of SDM to conservation problems

Any conservation planning requires reliable information on the spatial distribution of biodiversity and the gaps in the geographical coverage of locational information can very negatively affect conservation planning. A source of this information are observation records of species occurrences. A species observation record is a direct evidence of the species presence at a given geographic location. Unfortunately, the geographical coverage of such information often is far from complete and most of the regions identified as high priority for conservation are data-deficient. As a result of deficiencies in coverage creating lack of adequate spatial data, a species may incorrectly appear to be absent from a particular location, where in fact it does occur, simply because that location has never been surveyed (so-called false-absence). A traditional form of the knowledge on species distributions are species range maps, and these maps have been in use for long time as the major source of information for conservation planning. These maps provide a broad interpolation of species distributions, which is useful for coarse-scaled conservation assessments. When spatial units in an assessment are large enough to contain survey data, false-absences rarely are a problem. However, the range maps become of little use for fine-scaled regional planning because when spatial units are small, usually only a small proportion of them is surveyed. When we subdivide a large spatial unit used for coarse-scaled conservation assessment into many smaller grid cells, and a species is recorded as occurring in one or a few of those smaller cells that were surveyed, the species is assumed to occur in the remainder, but in reality, this is rarely true because a species may have a patchy distribution within a large unit and be absent in large part of it due to lack of suitable habitat or for other reasons. Thus, usage of range maps at fine spatial scales introduces a new type of a problem involving false-presences.

Any assignment of occurrence records to grid cells superimposed on an area of interest inevitably involves either false-presences or false-absences, or both. When we reduce the grid cells to which occurrence records have been assigned to minimize false-presences we also simultaneously increase the frequency of false-absences, particularly if the survey density and coverage are poor. As a result, "where conservation planning decisions need to be made at a relatively fine spatial scale in regions with sparse biological data, it may be impossible to find a cell size for representing biological distributions that keeps both false-absence and false-presence rates acceptably low" (Ferrier 2002). Modeling distributions of individual species allows not only filling the geographical gaps in information on species distributions, but also reducing the frequency of false-absences inherent in species occurrence datasets, while at the same time avoiding the increased frequency of false-presences incurred by using coarse-scaled range mapping (Ferrier 2002; Rondinini et al. 2006).

In SDM this is done by linking, through a derived statistical model, available data on species presences/absences with mapped environmental variables such as climate, substrate or topography, and then extrapolating the results on unsurveyed areas. This advantage

of SDM to provide geographically complete information for conservation planning has been immediately recognized, and the application of SDM to biodiversity conservation became one of its most important uses since the early stages of this discipline development (Franklin 1995; Guisan & Zimmermann 2000; Ferrier 2002).

The sections below show how SDM, due to the features outlined above, and superiority of SDM-predicted maps of habitat suitability over species range maps, can be successfully applied to various conservation problems.

Locating previously unknown populations of rare and endangered species

Locating populations is often a difficult task when target species are rare and/or poorly known. Very intensive field surveys may be required if the species requirements are poorly understood, population sizes are small and individuals are scattered over large areas. In addition, surveys can be further complicated by political unrest or low area accessibility. These problems are particularly frequent in species rich but poorly known tropical regions where distributional data are scarce.

SDM provides a powerful predictive framework for targeting areas for field surveys to locate unknown populations (Bourg et al. 2005; Jarvis et al. 2005; de Siqueira et al. 2009; Williams et al. 2009; Lomba et al. 2010; Särkinen et al. 2013; Fois et al. 2015; McCune 2016). By narrowing down a search area only to locations with a high probability of species occurrence, SDM can considerably increase the chances of population discovery while greatly reducing labor and time spending.

An example of SDM application for locating unknown populations is a study of Menon et al. (2010) done on *Gymnocladus assamicus*, a critically endangered tree species endemic to northeastern India known from only 14 populations of 1 to 7 trees each. The used two different algorithms gave similar predictions of suitable areas, and averaging their results produced a map with 26 discrete areas having the highest probability of species occurrence. A field survey organized in 14 more easily accessible than the other 12 sites located 5 new populations of *G. assamicus*.

Another example is provided in Särkinen et al. (2013). A study species, *Solanum pseudoamericanum*, was originally known from only four locations in southern Peru and its distribution was thought to be restricted to the seasonally dry tropical forests of this area. The authors used these four species occurrences as input in SDM to predict the most favorable for the species locations to be targeted for search of other populations. In the analysis, the model was fitted using southern Peru alone, and then projected over the whole Peru territory. Limiting the area extent when fitting the model was supposed to prevent overfitting and underestimating the potentially suitable area. Areas with a relative suitability above 40% were considered priority areas for population search. SDM results extended the species potentially suitable range to northern and central Peru, and a field trip in 2013 to these areas discovered 17 new populations of *S. pseudoamericanum* (Fig. 3). The new SDM then utilized the occurrences of 21 populations plus the locations of 5 verified herbarium specimens and used the entire Peruvian territory for both model fitting and projecting. This SDM narrowed down the predicted in the previous analysis suitable area (Fig. 3), proving the usefulness of iterating SDM with SDM-informed field searches.

Assessment of species endangerment status

When developing conservation programs, it is necessary to know for each target species its conservation status, that is, the risk of its extinction on a global and national scale. Conservation status assessments are usually done using a set of criteria developed and published by the International Union for Conservation of Nature (IUCN). Based on these criteria, a species is assigned to one of several categories of the IUCN Red List. Nowadays, SDM is incorporated into these criteria as a way to estimate the species range size, but usage of SDM in species range assessment has both *pros*

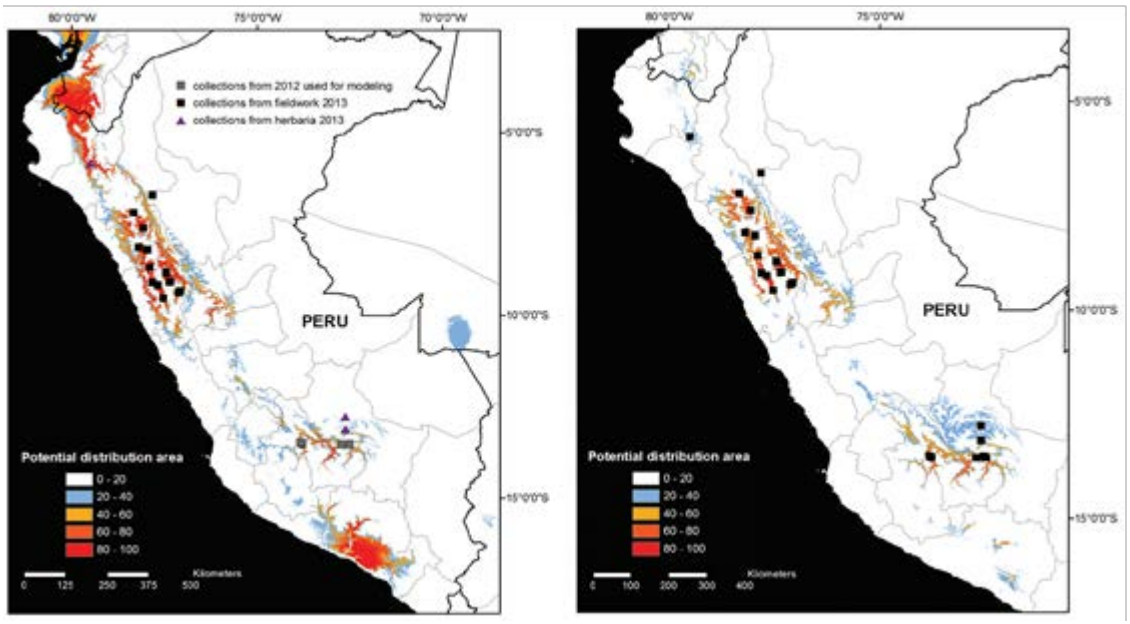

Fig. 3. Application of SDM for locating unknown populations of *Solanum pseudoamericanum* (from Särkinen et al. 2013). Left panel: Habitat suitability map produced using four localities known by 2012 (grey squares). In 2013, the areas identified as highly suitable were visited and as a result 17 new localities were discovered (black squares). Five additional collections were identified from the herbarium loans (triangles). Right panel: Habitat suitability map produced using all currently known 26 occurrence records.

and *con*s. The major *pro* is that SDM may have no alternative when actual occurrence data are scarse or fragmentary. The *contras* are that it can easily overestimate the actual range size when a suitable habitat is unfilled due to dispersal limitations, barriers in the landscape, or local extirpation by predators, competitors or humans, or underestimate the actual range when the species niche is only partially covered by known occurrences. Below we will consider, using examples from the literature, how exactly SDM can be used for assessment of species conservation status.

Extent of species range as a risk assessment criterion

Two species distribution criteria proposed by IUCN, namely Extent of Occurrence (EOO) and Area of Occupancy (AOO), are of critical importance for evaluating the risk category to which a species classifies. These two estimates are globally accepted as surrogates for extinction risk under IUCN Red List criteria (Gärdenfors et al. 2001).

EOO is defined as the area delimited by the shortest continuous imaginary boundary encompassing all known locations of the present taxon occurrence. This parameter measures the spatial spread of the occupied by a species areas and, according to the IUCN recommendations, should not be interpreted as either a measure of the species range or as an estimate of occupied or potential habitat. Rather, it measures the degree to which risks from threatening factors are spread spatially. In simple words, of two sets of populations identical in size and number, one confined to a smaller area will be at higher risk of extinction. EOO is usually calculated as a convex hull, which is defied as the smallest polygon in which no internal angle exceeds 180˚ and contains all sites of occurrence.

Because the area delimited as EOO almost always contains unsuitable or unoccupied habitats, a more objective measure of a species range is AOO, the area of suitable habitat within EOO currently occupied by a taxon. AOO is usually quantified by counting the number of occupied cells in a uniform grid of an appropriate scale (2 x 2 km) that covers the entire range of a taxon (IUCN 2017). According to criterion B of IUCN, a species is classified as vulnerable (VU) for AOO smaller than 2000 km^2, as endangered (EN) for AOO < 500 km^2 and as critically endangered (CR) for AOO < 10 km^2. In addition to these thresholds, two of the three sub-criteria must be met (whether a species is severely fragmented, or is continuously declining, or extremely fluctuating). EOO and AOO can be routinely obtained through Geospatial Conservation Assessment Tool (GeoCAT), a browser-based and easy to use tool for rapid geospatial analysis and Red Listing assessment (Bachman et al. 2011; Moat & Bachman 2017).

When a species is well studied and its occurrence database is thorough and complete, reliable estimation of EOO and AOO is straightforward. However, in many regions of the world, species ranges are poorly known or documented. For such cases, IUCN recommends that EOO and AOO "should not only include the actually known sites, but also inferred or projected sites" (IUCN 2017), i.e. IUCN encourages the application of SDM for delimitation of EOO and AOO. Following this recommendation, SDMs were used as an alternative measure to EOO (Sérgio et al. 2007; de Castro Pena et al. 2014; Syfert et al., 2014), to AOO (Jiménez-Alfaro et al. 2012; Marcer et al. 2013) or both (Cardoso et al. 2011; Attorre et al. 2013; Muñoz-Rodríguez et al. 2016). However, the limitations of using SDM for estimating EOO and AOO must be understood. Since SDM predicts a potentially suitable habitat rather than a species realized niche, in majority of situations it will over-estimate the species ranges (Sérgio et al., 2007; de Castro Pena et al., 2014; Fivaz & Gonseth, 2014), being too optimistic approximation of the latter. Among the studies that evaluated usefulness of SDN for delimitation of EOO and AOO, two deserve mentioning, Breiner et al. (2017) showed that EOO and AOO based on spatial projections of SDMs poorly capture local extinctions and the modelled range sizes can even increase when up to 50% of the occurrences are removed by simulated extinction events. Attorre et al. (2013) conducted an intensive search for seven endemic tree species of Socotra island to ensure that the information on species distribution was accurate and complete, and then used all known species occurrences in SDM. The habitat suitability maps were produced using a threshold of 0% omission error, i.e. not allowing any observed presence to be incorrectly predicted. Based on their results (Fig. 4), the authors concluded that SDM cannot be used as an alternative to traditional topological methods for estimating EOO and AOO. This conclusion seems to be well justified, since the authors conducted such a thorough survey of study species locations, that a possibility that some extant populations were unaccounted for is very unlikely. Although the results of the above two studies do not negate usefulness of SDM for IUCN assessments completely, they are an alarm warning against uncritical usage of SDM-based EOO and AOO.

A good example of how SDM-derived estimates of EOO and AOO can be used in conservation is a study of Marcer et al. (2013). Marcer with colleagues conducted SDM for seven well studied Mediterranean endemic plant species having >10 occurrence points per species. The authors derived binary maps of potentially suitable areas in combination with EOO calculated as a convex hull polygon. For all but one species, the potentially suitable area was much larger than the occupied range (Fig. 5). However, the authors did not interpret the potentially suitable area as EOO. Instead, they interpreted the area of overlap between SDM-predicted suitable area and EOO as the geographic equivalent of species realized niches and AOO (Fig. 5). Although such interpretation still appears to be an overestimation, for poorly studied species whose known populations are scattered over a

large area, this way of SDM usage for estimation of AOO does make sense, at least as a first approximation of a true AOO.

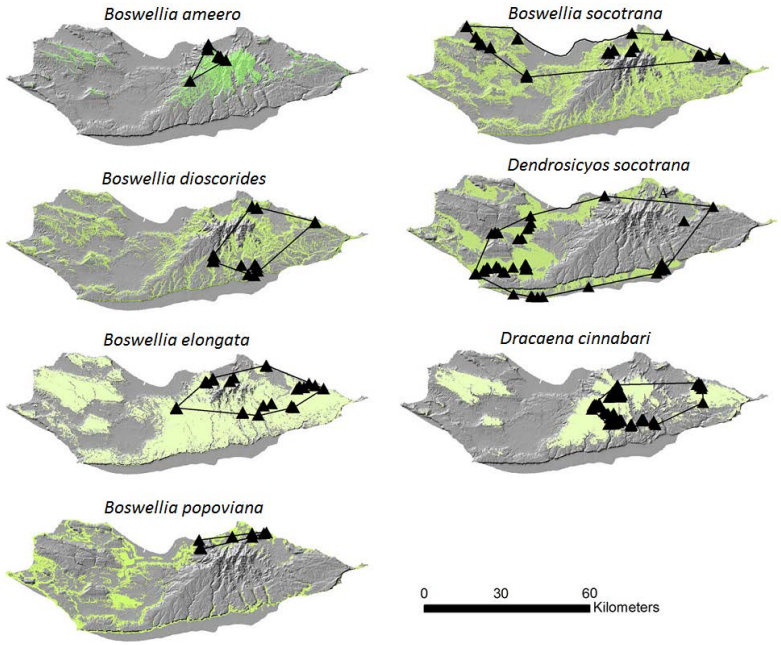

Fig. 4. Predicted suitable area (light green), occurrences (black triangles) and Extent of Occurrence calculated with the minimum convex polygon method (black connected lines) for 7 Socotran endemic threatened tree species (from Attorre et al. 2013).

Predicted change in a species range as a risk assessment criterion

SDM was recognized by IUCN as a tool not only for estimating EOO and AOO as described in the preceding chapter, but also as a tool to assess the species vulnerability to climate change (IUCN 2017). Technically, this can be done by estimating the expected reduction in suitable habitat. An example of such SDM application is the study of the range changes of *Gentiana lutea* known from 24 localities in Sardinia by Fois et al. (2016). Comparison of the habitat suitability maps predicted under current and expected future climatic conditions revealed a significant (>50%) reduction in the species EOO by 2070 (Fig. 6), with all local extinctions occurring at the edge of the species distribution and at the lowest part of the elevation gradient. A predicted reduction in EOO greater than 50% within a time period lower than three generations classifies *G. lutea*, according to the sub-criterion A3, as belonging to the EN category (IUCN 2001, 2016).

Distinguishing historically rare and anthropogenically rare species

In the 90th, following Rabinowitz (1981) distinction of different types of species rarity based on geographic range, habitat specificity and local population size, two conservation biologists looked at the species rareness phenomenon from a different angle. Huenneke (1991) and Fiedler & Laven (1996) proposed that rarity can be the result of two very different causes. One is an inherent rarity due to a vary narrow ecological niche. Although humans could contribute to decline of these species, they have never been widespread or common. Another one is rarity caused exclusively by anthropogenic activity being it direct harvesting or destruction of their habitat. In contrast to the inherently rare species, this kind of species

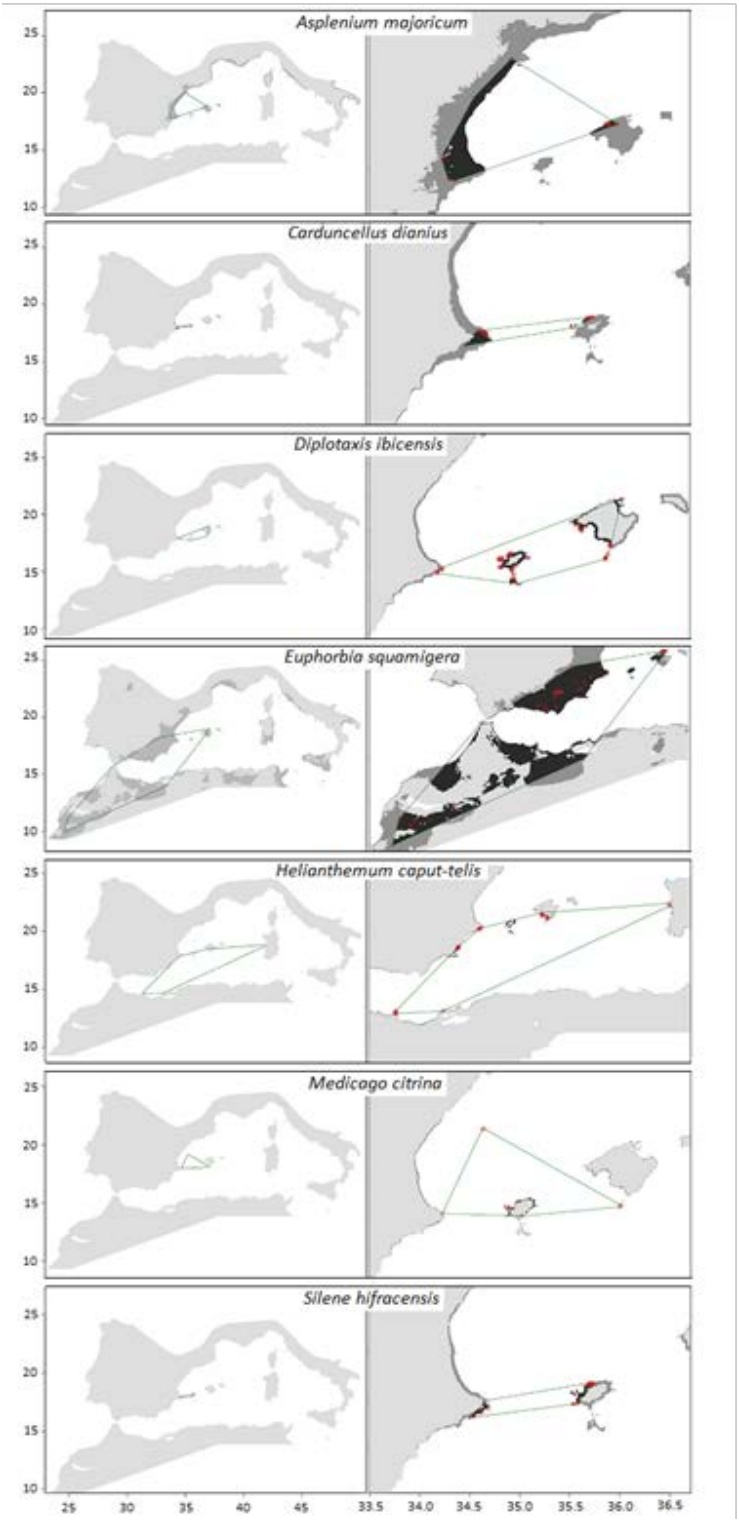

Fig. 5. An overview map (left) and close-up map (right) of the Extent of Occurrence (EOO) calculated as convex hull polygon (green lines) and potentially suitable area identified via SDM (dark grey areas) for seven western Mediterranean plants (from Marcer et al. 2013). The red dots indicate occurrences. The black areas denote the potentially suitable area within EOO, which are interpreted by the authors as Area of Occupancy (AOO).

became rare only recently after disappearance of once common natural settings. Many rare species that we know today can be assigned to the same rareness category *sensu* Rabinowitz (1981) based on their current geographic range, population size and presumed habitat specificity, but this would be misleading because their former (prior to the anthropogenic impact) range and population size could be dramatically different form the current ones.

Habitat specificity, the clue to distinguishing the rareness type, is very difficult to ascertain when the number of known populations is small. Volis and Tojibaev (2022) showed that habitat specificity can be surmised from the extent of the range predicted implications. One is that the SDM predictions for historically rare species can be regarded as indeed very close to the true species critical habitat. This stems from the fact that the predicted suitable area was less than 50 km^2 for 32%, and less than 200 km^2 for 64% of the species studied. On the other hand, the SDM-predicted range for anthropogenically rare species is apparently an overestimation of the latter. This does not mean that SDM predictions for species representing the second group are of no value for defining species critical habitat. They are, but delimitation of the true critical habitat for these species will require additional efforts in terms of expert knowledge to narrow down (and for some species substantially) the area predicted by SDM as suitable. Another important conservation implication this study findings will find in the practical conservation actions prescribed to endangered species. Imperiled species from the first category are less amenable (if at all) to such conservation actions as trans- or relocation. This means that there is no alternative to protecting the last existing populations and restoring (if necessary) the habitat of these populations. Species from the second group can potentially grow in many more locations than they currently occupy, and therefore, for these species, translocation can be the most appropriate strategy when their last by SDM, even if the number of known species occurrences is extremely small. In their study, SDM was applied to 50 critically endangered plant species of Uzbekistan. Although all studied species were extremely rare, the extent of their predicted critical habitat ranged from 2.6 to 15,508 km^2 and did not correlate with the number of occurrence records. The authors concluded that the extent of the threatened species predicted suitable area can be used as an indicator of whether the species rarity is inherent due to vary narrow ecological niche or is caused solely by anthropogenic activity. The distinction between historically rare and anthropogenically rare species made from SDM predictions has several important conservation remaining locations are degraded or can not be protected for whatever reason. This is illustrated in Fig. 7, which shows the predicted distribution for the congeners of *Allium* and *Tulipa*, all of which are Category 1 but differ sharply in their predicted suitable range, and therefore fall into either the first (*A. decoratum*, *T. orythioides*) or the second category (*A. rhodanthum*, *A. majus*, *T. uzbekistanica*). The aforementioned species, representing the second group of anthropogenically rare species, grow in habitats that are more accessible to humans, or have properties that make them more attractive to humans. For example, having wide predicted range *A. rhodanthum* grows in heavily grazed lowlands, while *A. majus* not only grows in low altitude areas used as pastures, but also is intensively collected as a food plant. In contrast, having narrow predicted range *A. decoratum* grows in mountainous areas above 2500 m, which are seldom visited by humans. Likewise, having a very localized predicted range *T. orythioides* grows at an altitude of 2500-3000 m, while having a wide predicted range *T. uzbekistanica* occupies lowland areas. Future research should thoroughly test for a relationship between the two types of rarity and the extent of the SDM-predicted range.

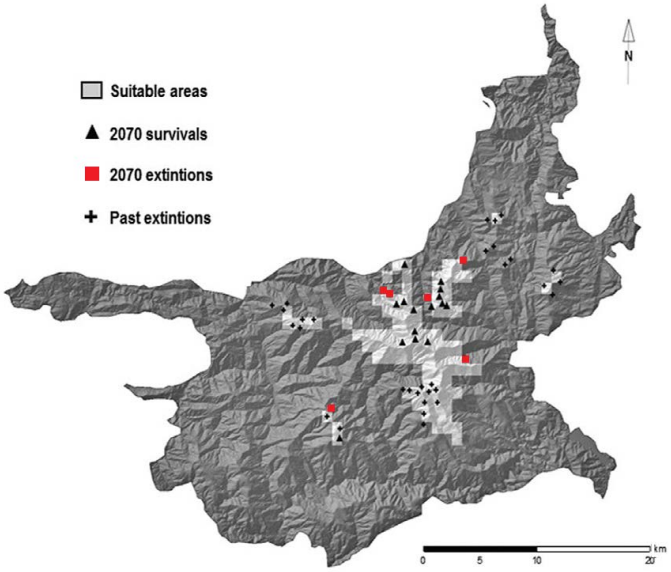

Fig. 6. Estimated changes by 2070 in habitat suitability for *Gentiana lutea* in Sardinia based on RCP 8.5 emission scenario (from Fois et al. 2016).

Area prioritization for protection

Usage of species richness maps

Species richness maps are widely used for assessing spatial biodiversity patterns, knowledge of which constitutes an important component of conservation planning an

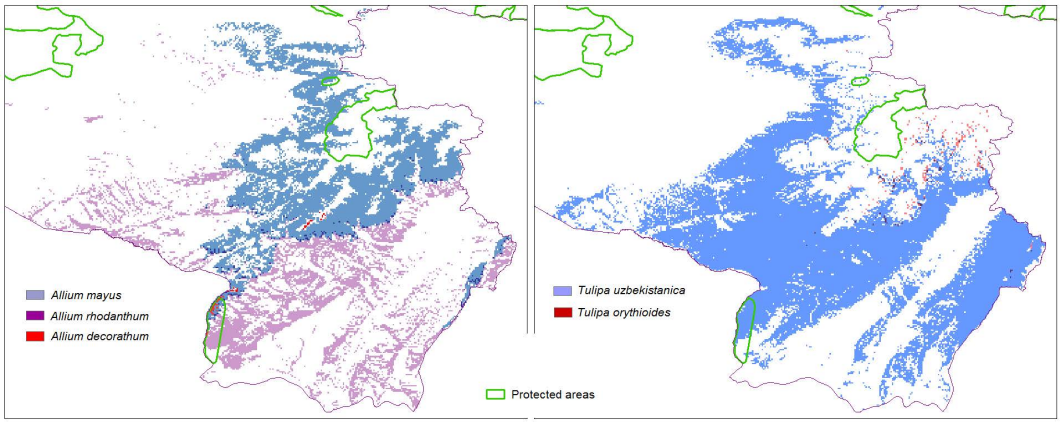

Fig. 7. SDM-predicted suitable habitat for several critically endangered *Allium* and *Tulipa* species in Uzbekistan illustrating a difference between historically rare and anthropogenically rare species (from Volis and Tojibaev 2022).

Klorvuttimontara et al. 2011). However, the use of species richness alone is insufficient to prioritize areas for conservation (Fleishman et al. 2006), because other aspects of biodiversity, such as endemism and endangerment are in many cases even more important. Thus, the use of information on the spatial distribution of

threatened or endemic species in addition to species richness maps can provide a better picture of the effectiveness of the protected area network and aid in the identification of candidate conservation areas (Chape et al. 2005; Thorn et al. 2009; Koch et al. 2017).

Koch et al. (2017) is a case study of how to determine areas of high conservation importance by combining SDM-informed maps of plant diversity hotspots and threatened species. The study area was poorly studied Caatinga ecoregion, the only exclusively Brazilian biome. Currently, less than 1% of this area is strictly protected by a network of nature reserves, national parks and ecological stations. The authors used stacked species distribution modelling (S-SDM) to produce a map of predicted floristic species richness from individual SDMs for 1,062 species, and maps of predicted distributions for 27 threatened plant species, and then combined the diversity hotspots and hubs of threatened species to derive spatial units of high conservation importance for each of eight sub-ecoregions. Identification of these areas utilized the average number of species per sub-ecoregion as a threshold value. Raster cells below the calculated thresholds were labeled as areas with "low" conservation importance. Map cells with the number of species in the sub-ecoregion above the threshold were categorized into three other categories of conservation importance: high (species richness threshold, SR), very high (endangered species threshold, THR) and extremely high (both thresholds, SR + THR). The final map (Fig. 8) depicted the richest in plant diversity and endangered species areas in each sub-ecoregion, providing complementary information for prioritizing potential candidate areas for protection. These identified areas made up 24% of the entire Caatinga region, whereas only 7% of the biome is currently protected.

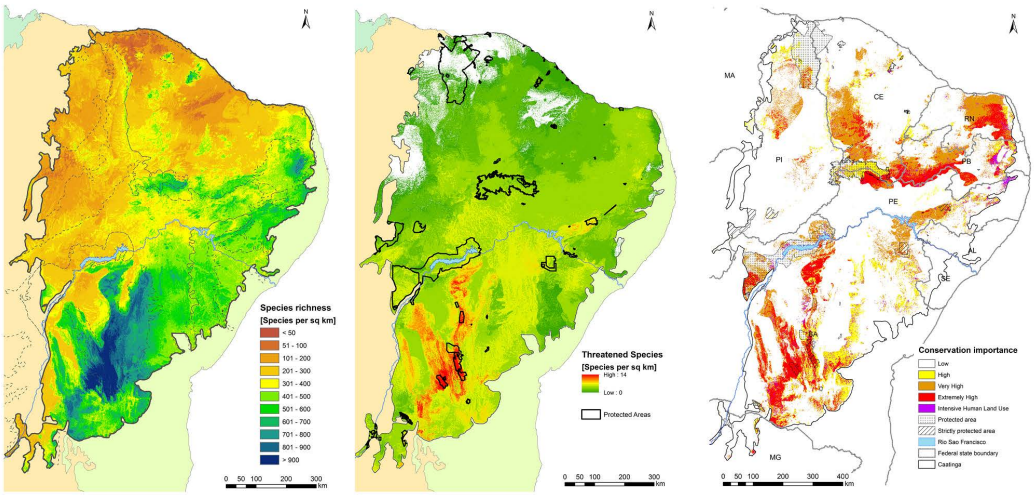

Fig. 8. Geographic distribution of predicted floristic richness (left panel), threatened species richness overlaid with protected areas (middle panel), and priority areas for plant conservation (right panel) in Caatinga ecoregion of Brazil (from Koch et al. 2017). Based on mean species number and threatened species number values per sub-ecoregion the map cells were categorized into four categories of conservation importance: (a) low, (b) high (SR threshold), (c) very high (THR threshold) and (d) extremely high (SR + THR threshold) (see text for explanation). The two letter abbreviates are federal states.

The next example shows how SDM-informed species richness maps can be produced at substantially higher resolution. Lannuzel et al. (2021) used high-resolution (10m and 30m) topographic variables to model distribution of 23 rarest plant species from Mount Kaala, a hotspot of narrow endemism in New Caledonia. The MAXENT output with the habitat suitability values for 23 species was used for conservation priority scoring. Each raster cell of a map received a composite species richness score taking into account three criteria: IUCN endangerment status, endemism and the vegetation type rarity. The resulting scores ranged from 0 to 3 (Fig. 9).

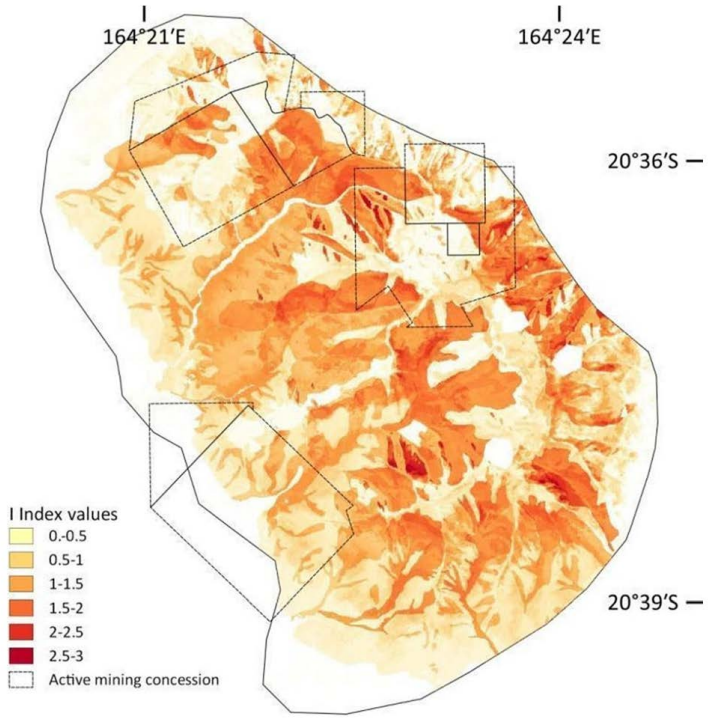

Fig. 9. Distribution of priority areas for conservation (computed with the composite I index) at Mt. Kaala (New Caledonia) (from Lannuzel et al. 2021). In the I index higher values get areas with higher number of rare plant species weighted according to IUCN status, endemism status and habitat rarity.

Integration of SDM and site-selection algorithms

Any regional conservation planning includes as a goal the creation of a network of protected areas in which all local species are represented and efficiently preserved. The prioritization of areas for protection is nowadays done using computer-based reserve selection algorithms implemented in devoted software such as Marxan, Zonation or C-Plan.

Ideally, these selection algorithms rely on complete, high-quality information on the spatial distribution of biodiversity. For some regions like Europe or United States, such information exists. However, for most regions of the world and virtually all biodiversity-rich countries, this information is far from complete. When species distribution data are fragmentary, spatially biased, or incomplete, SDM species range predictions are used instead of real data in reserve selection algorithms (e.g. Cuesta et al. 2017; Taylor et al. 2017; Choe et al. 2018;

Spiers et al. 2018). Several studies have proven that the integration of SDM and site-selection algorithms is a powerful tool for reserve design.

To be useful for reserve selection algorythms, the direct output of the SDM software, which are continuous values of habitat suitability ranging from 0 to 1, must be converted into predicted occurrences. There are two drawbacks of using direct output from SDM analysis for reserve design. First, the same habitat suitability value (e.g. 0.5) can indicate very high suitability for one species but very low for another. Another is that a suitability value below a certain threshold for a given species has no meaning, i.e. must be zero. These problems can be solved by converting SDM predictions to binary values of 1 (suitable) and 0 (unsuitable) habitat that are biologically meaningful and comparable across species.

Manish & Pandit (2019) used a combination of SDM and reserve design modeling for delineating and prioritizing areas for conservation of endemic plant species under current and future climatic conditions in Sikkim Himalaya. The predicted by MAXENT suitable under current and future climate habitats for 584 species were used as input data in Zonation software to identify priority conservation areas in the region. The existing PA network in the region was found to be inadequate to protect the endemic plant diversity in both current and future climate scenarios. Based on these results, the authors proposed expanding the existing PA network by additional 896 km^2 and creating three new PAs.

Choe et al. (2018) assessed the representation of biodiversity in existing South Korea's protected areas as the average proportion of the predicted ranges of plant species that have been included in existing PAs. Suitable habitat was predicted for 2,297 plant species, of which 891 species had fewer than 10 occurrence points and 560 species with fewer than five occurrence points, using MARS algorithm. The optimization of the target conservation area, which would improve range representation of 2,297 plant species, was performed with Marxan software. It was found that the expansion of PAs to 15.3% of the mainland area, including existing PAs, would improve the overall plant species' range representation to an average of 16.8% for all species, to 30.2% for endangered species, and to 22.4% for endemic species. Although some identified priority conservation areas were extensions of or adjacent to existing PAs, many biodiversity hotspots with high species richness, in particular lowland coastal areas, were located well outside the existing PA network.

Lessmann et al. (2014) applied SDM in combination with a selection algorithm to identify new and complementary potential conservation areas in Ecuador that would increase the representation of terrestrial species diversity in the existing PA network. Given the lack of complete information on the distribution of the selected 809 terrestrial species of which, 182 were amphibians, 69 birds, 52 mammals and 506 plants, SDMs served as an intermediate step toward estimating their geographic distributions. The defined goals of the reserve selection were to include in the PA network the species-specific proportions of the extent of species range obtained from SDM. The latter proportions were defined based on extinction risk, taxonomic uniqueness and other criteria, and ranged between 15% and 30% of the SDM predicted species ranges. For each planning unit, Marxan determined two aspects: the conservation priority (urgency of protection based on the importance for preserving biodiversity and the risk of environmental degradation) and the feasibility of establishing an area as a reserve. As a result, it was found that the current network of PAs in Ecuador contains large conservation gaps and needs to be nearly doubled in size in order to effectively conserve regional biodiversity. As the country's government has set the goal of increasing the protected area to encompass an additional 5% of Ecuador's territory, the areas proposed in the first place included those with the highest priority and feasibility (areas with high importance, high vulnerability, high proportion of land under protection and high proportion of remaining natural vegetation), followed by

maximum priority and medium feasibility (areas with high importance, high vulnerability, high proportion of land under protection, and low proportion of natural vegetation remaining), and medium priority and maximum feasibility (high importance, low vulnerability, high proportion of land under protection, and high proportion of natural vegetation remaining) (Fig. 10).

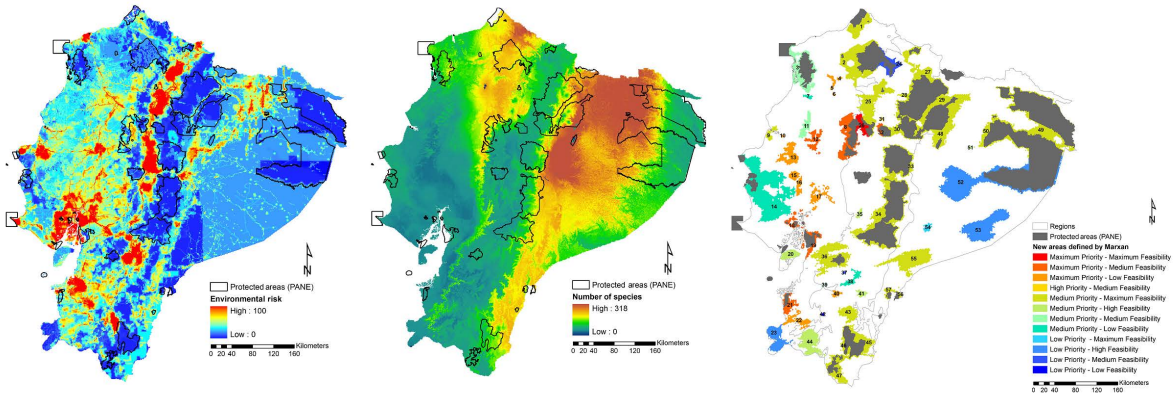

Fig. 10. Environmental risk surface (left panel), biodiversity richness based on predicted distribution of 809 species overlaid with protected areas (middle panel), and identified priority areas for conservation (right panel) in Ecuador (from Lessmann et al. 2014). The priority areas were chosen from the best solution in Marxan, employing classification according to the priority and feasibility assessments.

Kremen et al. (2008) have identified, using SDM and conservation planning, optimal expansion sites for promoting the persistence of Madagascar's biodiversity. The occurrence data for 2315 endemic species in six major taxonomic groups (ants, butterflies, frogs, geckos, lemurs, and plants) were used. The specific objective of the study was to prioritize areas to increase the country's PA to 10% of the country area and to optimally complement the existing network of nature reserves in Madagascar. To achieve this, the authors used as input data for the prioritization algorithm (Zonation), SDM predictions for 829 species with ≥8 occurrence records and point occurrence data for the remaining species. Narrow-range species and species that experienced a large range reduction between the years 1950 and 2000 were given higher weightings than the other species. The SDMs were performed with MAXENT using selected WorldClim variables and a forest cover variable. The multi-taxon solution to the intended target (highest-ranked 10% of the landscape) (Fig. 11A) was compared with the actual parks selected during the last protected-area expansion phase of 2002–2006, which increased the total reserve coverage from 2.9 to 6.3% of Madagascar (Fig. 11B). As the authors stated, the study provided important new insights into Madagascar's conservation needs and identified several previously overlooked regions with relatively low forest cover but considerable endemism as priority areas for protection. These regions have historically been ignored in favor of protecting large forests.

Reserve design and climate change effects

Selection algorithms in conservation planning must take into account the issue of climate change (Araujo et al. 2004; Hannah et al. 2007; Game et al. 2011; Krause & Pennington 2012; Bonebrake et al. 2014; Brambilla et al. 2017). On a large scale, this involves identification of the areas that are not only suitable for a defined species pool at the present time, but will also remain suitable in the future. These areas can be called climatic refugia because of their

ability to mitigate effects of climate change and thus safeguard the persistence of biodiversity (Game et al. 2011; Groves et al. 2012; Keppel et al. 2015). Given the importance of such areas, they should, whenever possible, be included in reserves and other categories of in a region is insufficient to conserve regional PAs.

If the number or size of potential refugia biodiversity, a solution can be establishing climate corridors, protected areas with natural vegetation, which would serve as a link between currently suitable areas and those that will be suitable in the future.

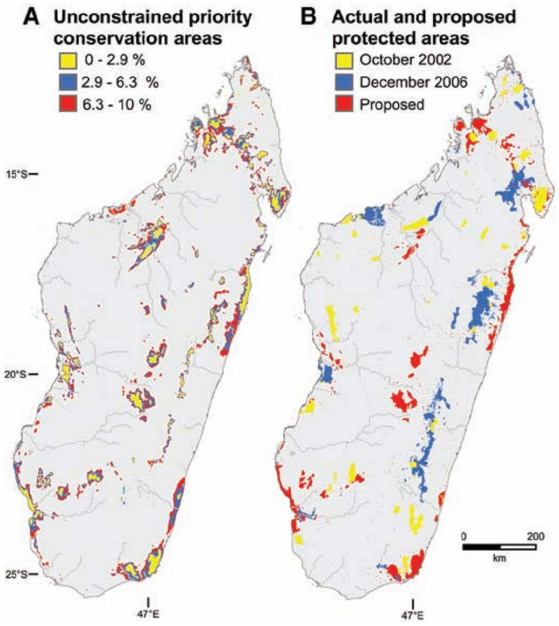

Fig. 11. Conservation priority zones in Madagascar (from Kremen et al. 2008). (A) Unconstrained multi-taxon solution, showing what would have been selected based on 2315 species if no areas were already protected. Colors indicate priority level: The top-ranked 2.9% priority areas are shaded yellow (equivalent to the area actually protected by 2002), the next-ranked priorities to 6.3% are blue (equivalent to the area actually protected by 2006), and the next ranked priorities to 10% (equivalent to the conservation target) are red. (B) Constrained multi-taxon solution, expanding (red) from existing parks in 2006 (yellow + blue = 6.3% of area) to 10% protection. The red areas are thus those that the analysis selects as the most important areas to consider for expansion of the current reserve network.

On a smaller scale, the problem of climate change can be solved by adjusting species ranges to changing climatic conditions. The latter can be achieved, depending on the species dispersal ability and landscape configuration, either by establishing corridors to connect existing populations, increasing suitable habitat at range margins, or through assisted migration into remote suitable areas.

An example of a large-scale study is the work of Baumgartner et al. (2018), which identified high richness refugia (refugia for ≥ 50% of representative species) in New South Wales, Australia. Their approach involved the following steps. First, the authors identified representative plant species within each ecoregion. An initial list of the 30 most frequently recorded native plant species for each of the six ecoregions was filtered to retain only those species noted as representative (characteristic, abundant, or otherwise prominent) of the state's floristic communities, and the resulting final list totaled 117 species (from 11 to 27 species per ecoregion). Occurrence records for each species were overlaid on a 1 x 1 km raster grid and reduced

to a single point per species per cell. Modeling was done for three time periods of 2000, 2030, and 2070. The used different climatic models that encompassed a range of equally plausible climate prospects were grouped according to their predicted impact into four scenarios: a hotter future with little change in precipitation; hotter and wetter; warmer and drier; and warmer and wetter. SDM was peformed to produce binary maps of suitable/unsuitable habitat for each representative species within each ecoregion. By excluding areas that were classified as suitable but for which no occurrence records existed, the authors assumed that these areas, although deemed suitable, do not contain extant populations of the target species and therefore can not represent true refugia for these species. Then, they calculated for each ecoregion a proportion of the number of representative for the ecoregion species for which suitable climate remains under each of the four climate futures. The identified refugia were areas projected to retain ≥ 50% of the ecoregion representative species (Fig. 12).

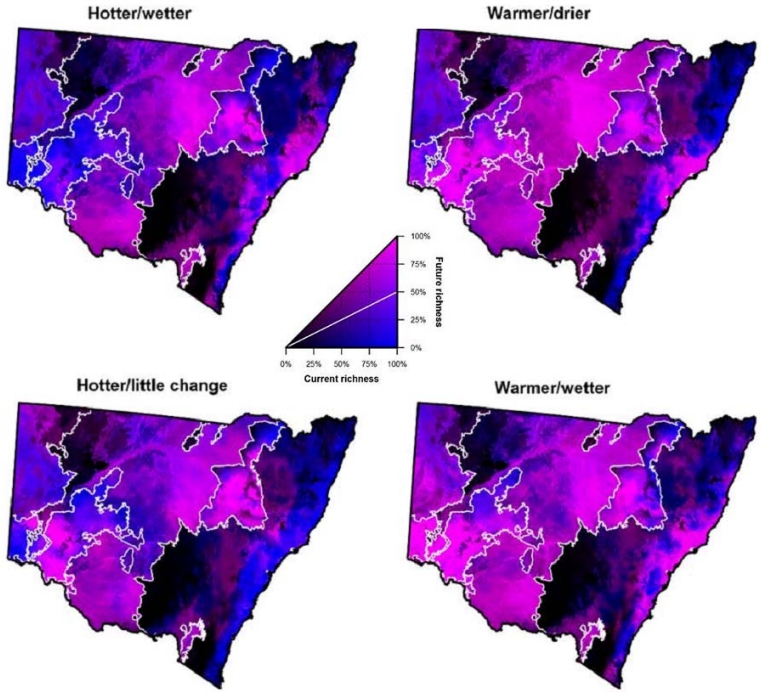

Fig. 12. Climatic refugia across New South Wales (Australia) under four future climate scenarios for 2030 (hotter, with little precipitation change; hotter/wetter; warmer/drier; warmer/wetter, compared to the average annual temperature and annual precipitation for the period 1990–2009) (from Baumgartner et al. 2018). Colours are interpreted as in the triangular legend, which shows current and future richness as a proportion of the number of representative species for each of the six ecoregions (which ranged from 11 to 27 species per ecoregion). Purple colours (above the white line in the legend) indicate that habitat is retained for more than 50% of initially occurring representative species, while blue colours (below the white line) indicate that habitat is lost for more than 50% of initially occurring representative species. Darker colours indicate that initial richness was low relative to the pool of representative species. Bright purple areas indicate high richness refugia (both current and future richness are high), and dark purple indicates low richness refugia (current richness is low but maintained into the future).

As a large-scale remedy for the anticipated negative impacts of climate change, Choe et al. (2017) have identified areas in mainland South Korea that would facilitate range shifts of multiple species. Identification of these potential climate meta-corridors involved modeling the current and future (year 2050) spatial distribution for 2,297 plant species grouped into five groups according to their spatial distribution, assessment of their spatial vulnerability, and creation of least-cost paths between the target areas where connectivity is required. Future species richness maps were constructed using model projections for four future climate scenarios. From the current and future suitable areas for the species in each distribution group, the authors estimated climate-driven group changes in species richness, and identified three of them as vulnerable to climate change. The species were assumed to disperse more successfully through

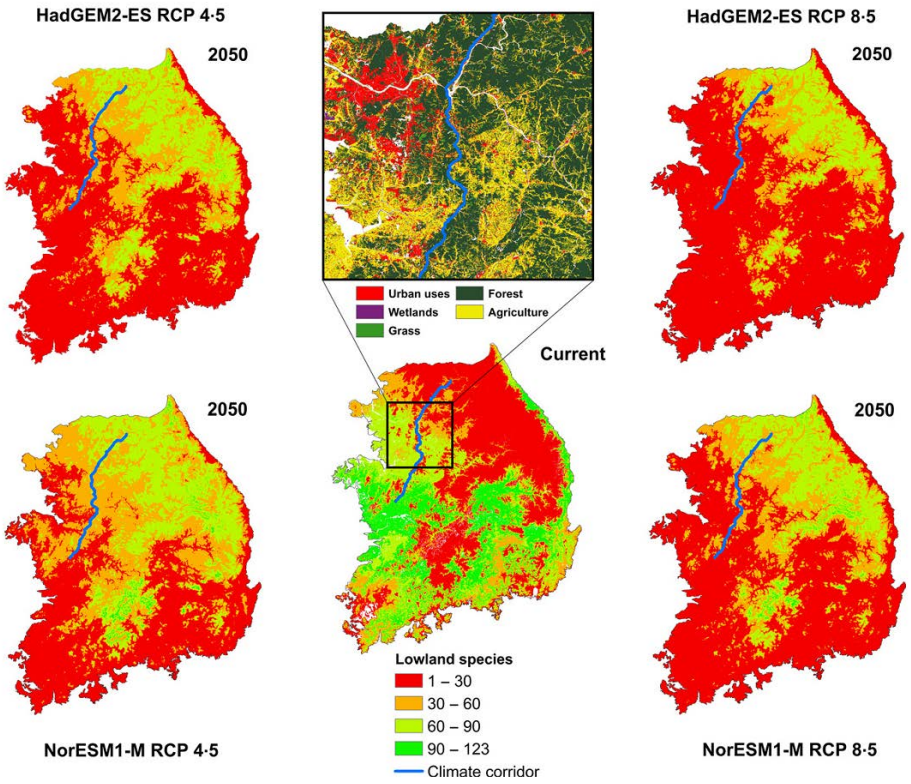

Fig. 13. Current and future species richness and a suggested climate corridor for lowland South Korea (from Choe et al. 2017).

areas containing suitable habitat, so the identification of these areas (i.e. meta-corridors) included the current land cover suitability in the corridor models. Each grid cell in a group was ranked by the density of neighboring cells within 5 km meeting selection criteria, and the cells with the highest value were selected as source and destination locations. Climate corridors were defined by connecting the current source and the future destination locations using the Cost Path toolbox in ArcMap. The main selection criterion for choosing source and destination locations for all groups was the top 20% of current and future species richness, respectively. The meta-corridor for one group (lowland plant species) is shown in Fig. 13. Beside identification of the meta-corridors, the authors provided for each of the three meta-corridors its unique policy implications: assisted migration for the highest elevation species for the montane group; significant

conservation and restoration work for the lowland group; and perhaps no direct intervention but monitoring to evaluate the effectiveness of the relatively intact habitats of the coastal mountain group meta-corridor.

In areas where climatic conditions change sharply over short geographic distances, the first-choice solution is poleward or altitudinally upward expansion of the reserve boundaries. For example, *Abies religiosa*, the preferred host for overwintering migratory monarch butterfly (*Danaus plexippus*) is currently confined to the Monarch Butterfly Biosphere Reserve (Mexico). The SDM model for *A. religiosa*, projected for a future (2030, 2060 and 2090) climate, has revealed that the predicted suitable habitat for *A. religiosa* will shift rapidly over a century and will move outside the reserve by 2090 (Sáenz-Romero et al. 2012). The extant populations in the reserve will not be able to track the climate change by shifting their range to higher altitude because they already occupy the highest elevations. A climate similar to today's will exist by 2030 only in areas with an altitude above 3275 m. Thus, the authors propose to realign the *A. religiosa* range to the expected climatic conditions by assisted migration to the flanks of the highest volcanoes in that area and designating these sites as protected areas (Fig. 14)

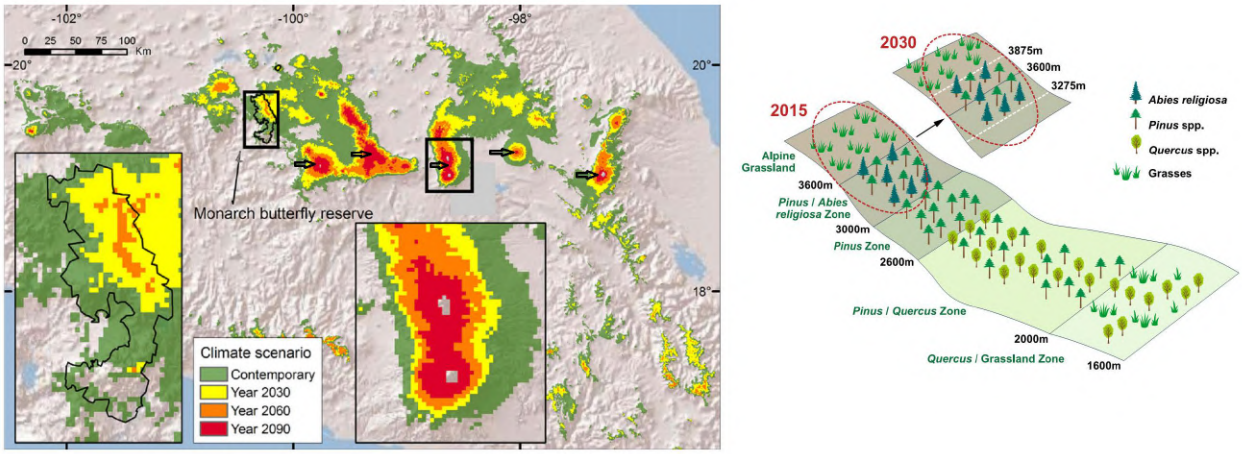

Fig. 14. Predicted range shift for *Abies religiosa* currently confined to the Monarch Butterfly Biosphere Reserve. The projected range shift of 275 m upward by 2030 is outside the current reserve boundaries, and therefore what is proposed to mitigate the effect of changing climate, is assisted migration to suitable sites indicated by arrows (from Sáenz-Romero et al. 2012 and Dumroese et al. 2015).

Augmentation, reintroduction and translocation

In situ conservation programs can utilize SDM to identify habitats in which introduced plants are most likely to survive and reproduce. For some species, identified locations will be within their historical range. For others, the historical range may no longer be available or have altered environmental conditions, while suitable conditions may exist elsewhere. In both cases, limiting planting to only the most suitable for a species locations will increase the chances of reintroduction / translocation project success. With the growing recognition of the utility of SDM for conservation, generated maps of suitable habitat are increasingly becoming an integral part of conservation plans fort threatened species (Powell et al. 2005; Shapcott & Powell 2011; Bonebrake et al. 2014; Wang et al. 2015; Rovzar et al. 2016; Swart et al. 2018; Guo et al. 2019; Tojibaev et al. 2019; Draper et

al. 2019), and IUCN/SSC (2013) recommends SDM as a standard tool for informing translocation. In two studies (Jusaitis et al. 2004; Draper et al. 2019), the reliability of SDM predictions was validated through in situ germination trials at sites with contrasting species suitability values. Several selected examples will illustrate how SDM can be used for *in situ* management planning.

Conroy et al. (2019) combined SDM with population genetic analysis to identify populations of the threatened tree *Fontainea rostrata* in eastern Australia that require some form of conservation management. SDM predicted that while southern populations of *F. rostrata* are likely to persist for the next 50 years, the more inbred and less genetically diverse northern populations will come under increasing pressure to expand southwards as habitat suitability declines. In order to enhance genetic diversity and maximize the likelihood of reproductive success, the authors recommended augmentation of existing, and especially the more isolated populations, as a priority management for *F. rostrata*. On the other hand, they recommended that future conservation efforts also include translocation to new sites to increase population connectivity, focusing particularly on areas identified as persisting in the face of climate change.

Cole et al. (2011) utilized SDM to justify translocation as part of a conservation plan for Joshua tree (*Yucca brevifolia*) inhabiting the North American Mojave Desert. According to the fossil records, Joshua tree had a much larger geographic distribution during the latest Pleistocene and experienced a sudden range contraction from the south as the climate became warmer in the early Holocene, leaving only what had been its northernmost populations. Today these populations demonstrate regeneration problems, and these problems can only exacerbate with increasing aridity. Cole et al. (2011) attempted to predict the future range of *Y. brevifolia* using the effects of a past warming event of similar rate and magnitude as an analog for the biological consequences of the expected in the near future climate warming. The authors developed a model of climatic suitability for Joshua tree and applied it to several models of future climates. All models predicted the future disappearance of Joshua tree throughout most of the southern part of its current range with only a few populations within the current range remaining viable. Several models identified new areas beyond the current range as potentially suitable, but the fossils have revealed that dispersal of the species in response to increased aridity, which happened ~11,700 years ago, occurred at a rate of only ~1 to 2 m/year. Such migration rate would be too slow to allow the species natural expansion into new climatically suitable areas. Nowadays the species is protected in Joshua Tree National Park, but 90% of the species suitable habitat in the park is predicted to be lost by 2100. Given the very low historical and current rates of species dispersal and the disappearance of Joshua tree's major dispersal agent, Shasta ground sloths, a solution is assisted colonization of already protected areas (Fig. 15).

Bonebrake et al. (2014) utilized a combination of SDM and population viability modeling to explore optimal conservation interventions under projected climate change, urbanization, and changes in fire regime for *Ceanothus verrucosus*, a Californian fire-dependent shrub. Populations in each habitat patch were simulated using an age-based stochastic matrix model based on empirically derived vital rates and assuming lack of natural seed dispersal between patches. The SDM predictions for various combinations of fire regimes, current and future climates, urban growth and management strategies were incorporated into population dynamics through patch-specific carrying capacity, which was a function of predicted habitat suitability. For each scenario, population dynamics were projected for 100 years. The authors found that under optimal fire regime, translocation of seeds is the best strategy to prevent population decline caused by urban development and climate change. Seed translocations performed better than seedling translocations because they did not need to be synchronized with uncertain fire events, while seedlings of *C. verrucosus*

emerge and become available only in the year of a fire. Even a simulated decade of moving 10% of seeds from a patch with a decreasing area of suitable habitat to patches

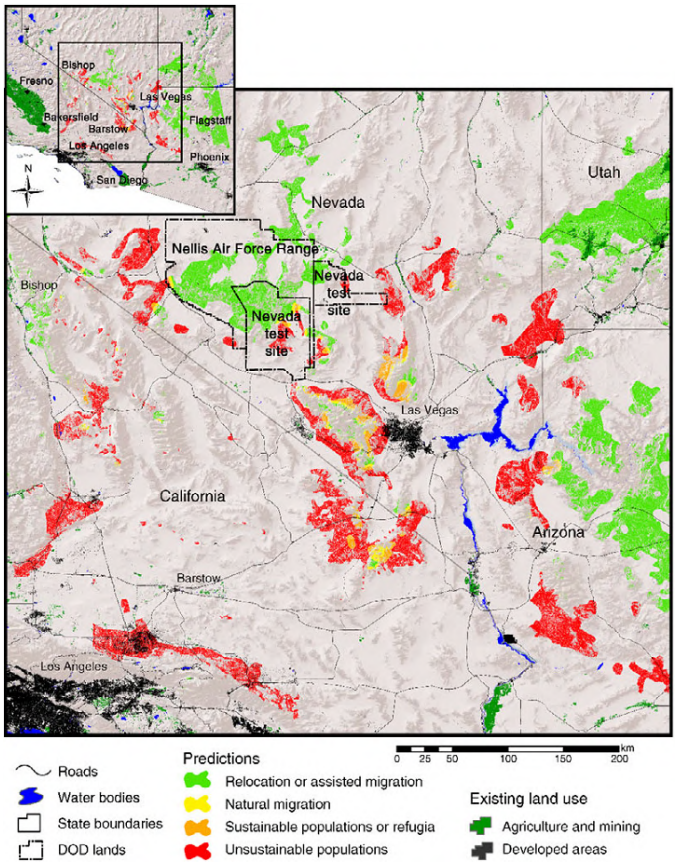

Fig. 15. Joshua tree (*Yucca brevifolia*) current and predicted in the future range (from Cole et al. 2011). Four different colors designate areas where SDM predicts existing populations to become unsustainable (red), remain viable (orange), migrate naturally and persist (yellow), or conditions suitable for assisted colonization in protected areas (green). DOD stands for the U.S. Department of Defense.

with increasing area of suitable habitat raised the total population size by as much as 75%. These seed translocations can be performed at regular intervals, accumulating a seed bank until a fire occurs, which acts as a germination cue.

Restoration

SDM has a wide range of possible uses in informing restoration plans. When information about historical vegetation communities is scarce or does not exist, SDM can predict which species can grow in a given location, or, alternatively, where a given species can find suitable conditions. If a goal is to replace invasive species with natives, SDM can identify areas that will become less suitable for invasive species in the near future and therefore have a higher chances of restoration success in comparison with other areas (Bradley et al. 2009).

Choosing a restoration site

SDM has great potential for restoration having conservation objectives, that is, when the goal is recreation of once existing vegetation community, and especially if the restored community is to be home to once abundant and

now rare species. For many regions that suffered from anthropogenic disturbance, the historical ranges of currently rare species are unknown, and locations where these species are currently absent may have potentially more suitable conditions than some of the locations where they are found today. Besides, there can be locations that potentially can harbor substantially larger number of such species than other areas. The search for such priority restoration areas can be efficiently conducted by SDMs.

One kind of such priority areas are habitats having more favorable and stable for local biota conditions in otherwise hostile environments due to the interaction between the complex terrain and the global climate. These habitats, called refugia, are important not only if they are pristine or almost pristine. Even partly degraded refugia are of high conservation value, and locating these areas has great practical importance for conservation. Favorable thermal regime and its stability over time is a feature of cool mountain environments in the tropics, which makes them areas of high endemism and important refugia for species under climate change. However, important parameters of the thermal regime, such as temperature maxima and diurnal temperature range are determined, beside elevation, by solar radiation, cloud and wind exposure and foliage cover. SDM, based on detailed meteorological data, allows modeling complex processes governing thermal regimes, and understanding the role of particular environmental features in these processes, and generating detailed predictions at large spatial scales.

Shoo et al. (2011) used SDM for prioritizing for the protection and restoration the cool refugia in tropical northeastern Australia. The region has a number of disjunct mountain ranges running parallel to the coast that support a diverse tropical biodiversity. The authors used the mean maximum daytime temperature as the dependent variable, and the altitude, latitude, distance to the stream, distance to the coast, foliage, solar radiation, cloudiness and wind exposure as predictors. Using the GLM algorithm, they were able to construct the spatial surface of the maximum air temperature, taking into account important climate-mediating processes. Then a one-dimensional temperature niche was determined for 153 native vertebrate species (26 mammals, 70 birds, 32 reptiles and 25 amphibians). Throughout the studied region, there was a strong attenuating effect of elevation, distance from coast and foliage cover on exposure to high maximum temperatures. In particular, the dense foliage cover typical of rainforests independently reduced temperature maxima by about 3°C during the hottest months. The foliage cover is a factor that can be directly influenced through management intervention. Therefore, the model was projected onto a deforested or degraded landscape, assuming that the foliage cover in this area was equivalent to that of extant rainforest and vine thicket vegetation, i.e. assuming that the rainforest was restored to its full historical extent within the region. The authors found that the core habitat of a disproportionately high number of endemic species (45%) was encompassed within just 25% of the coolest identified rainforest. In some areas of these critically important refugia, vegetation has been cleared of native vegetation. Incorporation of these areas into a network of PAs and reestablishment of their foliage cover through reforestation would bring disproportional conservation benefits via increasing the availability of cool habitat for local biota. Areas proposed for restoration (Fig. 16) will fulfill several tasks. They will increase the local extent of cool habitat, consolidate extant patches of remnant rainforest within thermally buffered environments, and facilitate dispersal between small and disconnected populations in this heavily fragmented landscape.

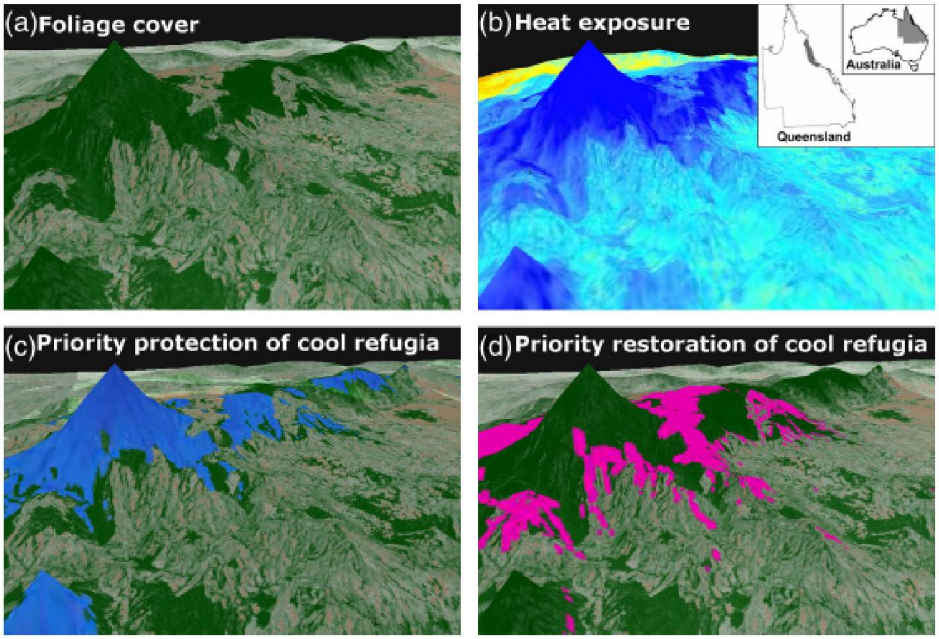

Fig. 16. Locating cool refugia within a modified landscape (from Shoo et al. 2011). Patterns of foliage cover (green, a) have a strong influence on buffering heat exposure (i.e. maximum temperature of the warmest period, blue to red, b). To increase the local extent of cool rainforest refugia, it is proposed to supplement the extant protected areas (blue, c) with formerly supporting cool habitat but currently deforested areas after restoration of their foliage cover through reforestation (purple, d).

Making species lists in restoration

Vegetation restoration projects usually utilize species assemblages derived from large-scale vegetation maps. A homogeneous species assemblage is usually assigned to the target site even if the latter exhibits substantial spatial variation. As a result, for a significant part of the restored area there can be a mismatch between the introduced species requirements and the local environment in which they are planted. The solution is defining species assemblages for restoration by modeling the distribution of individual species at an appropriate geographic scale. SDM, in which species environmental requirements are implicitly present, after overlaying habitat suitability maps for each listed species, will identify species assemblages for a spatial scale that reflects the target area spatial heterogeneity. This is illustrated by the three examples below.

In a study of Garcia del Barrio et al. (2013) the SDM-predicted distribution maps for 40 native tree species of Spain were used to identify species pools for ecoregions defined in two different ways at a spatial scale of 1 × 1 km. For each 1 x 1 km^2 grid-plot, conditions were considered suitable for a species when the predicted probability was above the threshold value of 10-percentile training presence. Species pools were determined for 52 forest landscape types and sub-types, as well as for 250 biogeoclimatic zones having distinct topography, vegetation and climate. Fig. 17 shows pools of identified species for selected forest landscape types that can inform species choices in restoration projects.

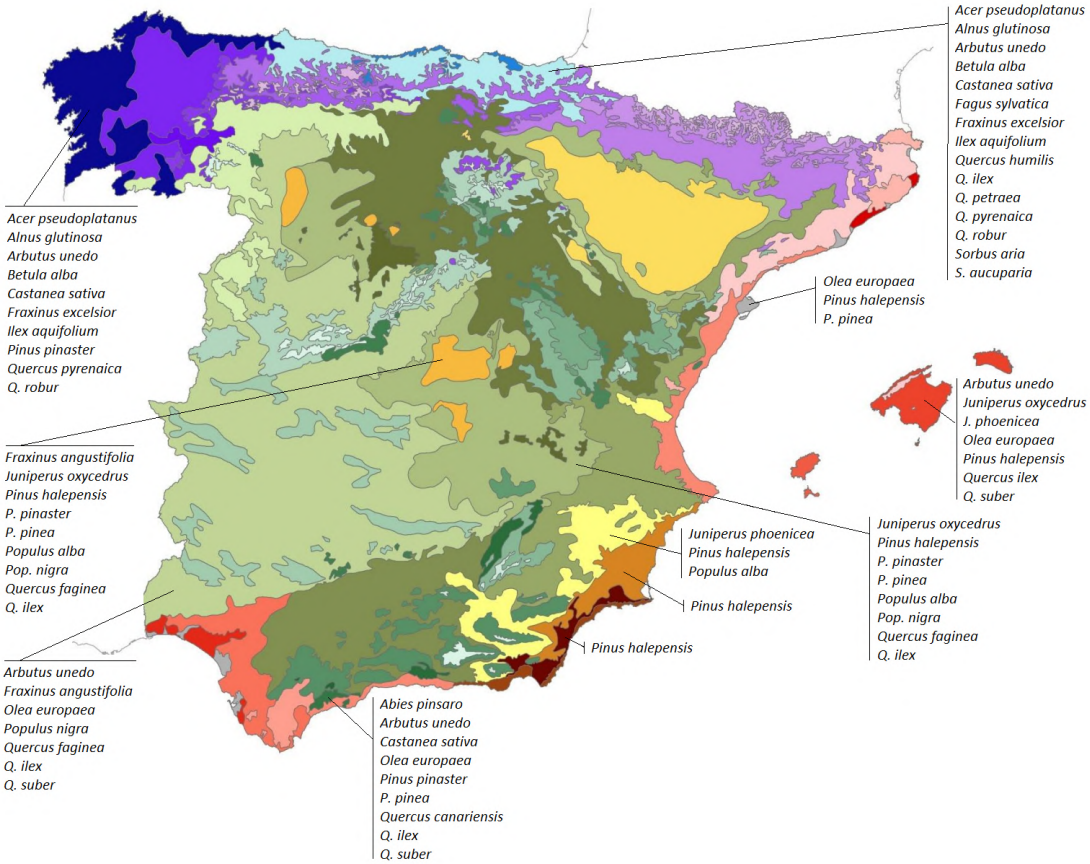

Fig. 17. Species pools identified by SDM for selected forest landscape types of Spain (modified from Garcia del Barrio et al. 2013).

In a study of Siles et al. (2010), also performed in Spain, lists of species for planting were worked out from the predicted at 100 × 100 m scale species assemblages. The burned-out area to be re-planted was divided into a grid of 723 squares of 1 ha each, and then characterized for the altitude, aspect, maximum slope, occurrence of a ravine or permanent watercourse, soil depth and percentage of rock cover, while the neighboring areas with well-preserved natural vegetation were surveyed to obtain a list of potential target species and to measure the same set of soil and topographic parameters as above. As a result of the survey, 36 native arboreal species were identified. Of these, 23 species, present in more than 5% of the plots, were chosen as target species for planting. Fig. 18 shows the SDM-predicted distribution of each species. It turned out that the superimposed distribution maps of individual species closely represent the regional natural vegetation in terms of species richness per unit area, environmental gradients in α-diversity, spatial variation in β-diversity, and frequency of species occurrence. The predicted vegetation map of the target area was also useful for diagnosing the state of recovery and for identification of sub-areas in higher or lesser need of restoration.

If the area to be restored has a fine-scale topographic heterogeneity, a resolution of even higher than 100 m may be required for modeling. In the study of Rovzar et al. (2016), suitability maps were created for 11 Hawaiian rare and endangered plant species at three scales: 1 km, 250 m and 10 m.

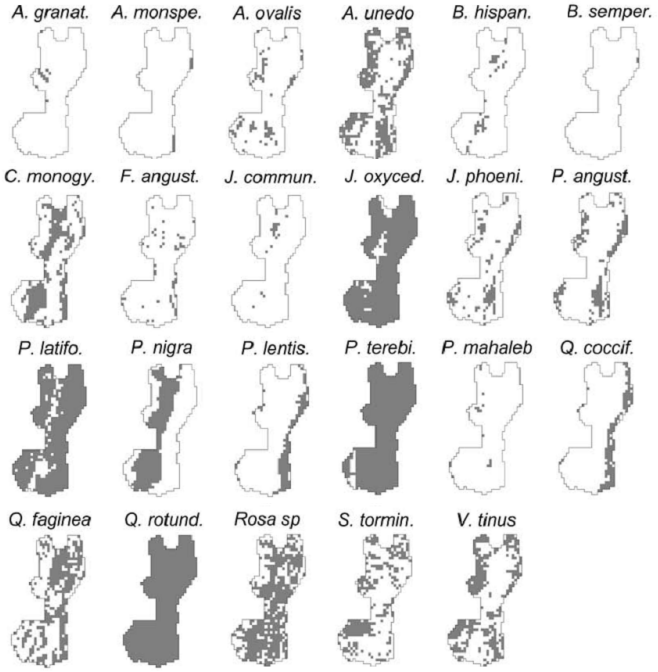

Fig. 18. Maps of predicted distribution for 23 plant species comprising a restoration species list, within a targeted for restoration area (from Siles et al. 2010). Cell size of the maps is 100 x 100 m.

The environmental variables included, in addition to climate and elevation, topographic variables slope and aspect, and soil. Information about soil (30 soil group categories) was available at a scale of 10 m. Other variables were downscaled to match this resolution. Soil and topographic variables were found to be more important for predicting habitat suitability across all species than climate, and the percentage of predicted suitable area was highest for most species at the finest scale of 10 m, indicating that similarities in micro-topography and soil within the studied area are better detected at finer scales. Areas where the habitat suitability maps for 11 species overlapped were regarded as having the highest chances of outplants' establishment, and the most cost-efficient. The areas of overlap for eight species, in total 1292 10 × 10 m plots (Fig. 19) were recommended for multi-species introduction.

Invasive species control

Alien invasive species are one of major causes of biodiversity loss and species extinction globally and therefore are a serious conservation problem. An essential strategy for the management of invasive species is prevention and early response in the event of invasion. Knowledge of environmental, and, first of all, climatic requirements of potential invaders, as well as the factors affecting the likelihood of establishment, is essential for predicting their spread. Analysis of these requirements that largely determine a potential of invasive species to adversely affect existing habitats and native biota, is an important area of conservation research. The ability to assess the suitability of a region for invasive species and the potential of these species to spread within it makes SDM a useful tool in invasive species risk analysis, monitoring, and control. Since prevention and early detection are the most important steps in the control and eradication of invasive alien species, SDM is increasingly being used as a tool in invasive species

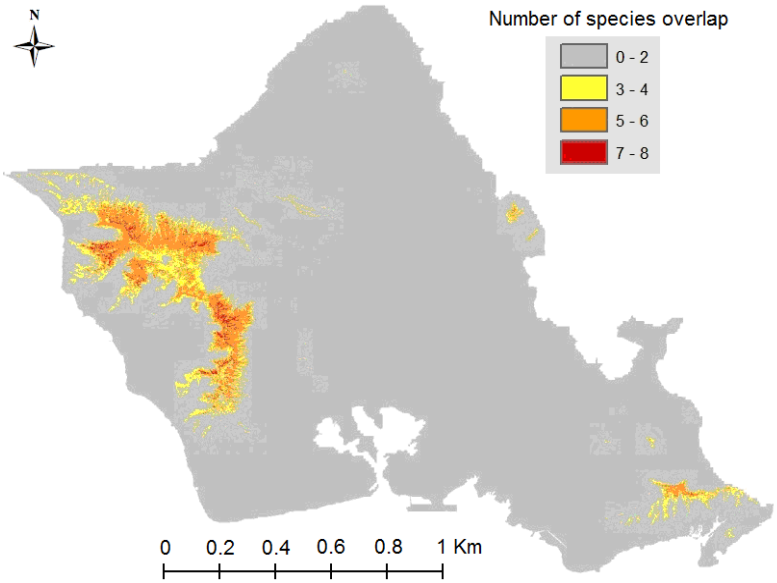

Fig. 19. Map of Oahu, Hawaii showing the overlap of the predicted distribution for 11 rare and endangered Hawaiian plant species (from Rovzar et al. 2016). Cell size of the map is 10 x 10 m.

management programs (Peterson & Vieglais 2001; Peterson 2003; Thuiller et al. 2005a; Wittenberg & Cock 2005; Crall et al. 2013; Lodge et al. 2016). Habitat suitability assessment by SDM allows determination of invasive species niche and identification of those areas that are more prone to colonization and therefore should be targeted for eradication efforts and for early detection of nascent foci (Thuiller et al. 2005b; Jiménez-Valverde et al. 2011).

Because the resources that can be allocated to control and eradication of invasive species are always limited, it is important to set priorities in terms of both, the species and the areas to focus on. Area prioritization is especially important, and identification of these areas is the most popular application of SDM in conservation as evidenced by the number of papers published.

Prioritizing species

In invasive species control, it is important to identify potentially problematic species and then prioritize them for management. Different methods exist for ranking the risks that each invasive species can cause; these generally focus on species biological characteristics and their potential biophysical impacts. Assessment of the species establishment risk can use the habitat suitability derived from SDM.

Renteria et al. (2017) used SDM in their assesment of the establishment risk for 25 plant species listed as eradication targets under South African regulations. Risk assessment criteria, in addition to the extent of the predicted potential range in the country, included the overlap of this range with biodiversity-sensitive areas and the feasibility of species eradication (the latter defined by the number of known localities and species eradication syndromes). The “eradication syndromes” approach combined three traits that define ease of eradication, length of juvenile period, seed persistence and dispersal functional group, into eight ordinal categories ranging from 1 = low eradication feasibility to 8 = high eradication feasibility. As a result, three management groups were identified. Of these, the group with a medium to high establishment risk and a high likelihood of eradication got the highest priority for eradication. The second priority group included species with a medium to low risk of establishment, but given the small number of known population and the species characteristics, the eradication of these species

is likely to be feasible. Finally, the species in the third group, although scoring a medium to high establishment risk, have a low chance of eradication due to the high number of known localities.

Prioritizing areas

One important component of alien species control is to predict the areas which an invasive species can colonize and where it can become naturalized, and for the latter SDM can be an invaluable tool. Some of these areas can be particularly prone to invasion, and, when these areas have high conservation value, they should be the first targets for invasive species management, being it prevention, elimination or control (Ibanez et al. 2009).

On a large regional scale, some areas called invasion hotspots pose a particularly high threat of being invaded by numerous non-native species. O'Donnell et al. (2012) identified such areas in Australia using individual SDMs for 72 taxa recognized as "weeds of national significance" in Australia under current and projected climates for 2020 and 2050. The generated maps of climatic suitability were combined by summing the values of projected climate suitability for all species in each grid cell. Two potential invasion hotspot regions

Another invasion-hotspot study (Duursma et al. 2013), also performed in Australia, focused on potentially invasive species (i.e. alien species that are documented as naturalized but not yet invasive). In this study suitable habitat was identified for 292 plant species under current and projected climates for 2035 and 2065. The 10% minimum training presence threshold was used to convert continuous predicted suitability values to binary. Hotspot maps at two scales: continental, and each of Australia's 37 ecoregions were generated by summing the binary maps for each species and reclassifying the grid cells with a summed habitat suitability that was equal to or greater than the top 25th percentile of all grid cells (Fig. 20). The locations of the invasion-hotspots predicted for naturalized but not yet invasive species in this study and for the most serious invasive plants in Australia (O'Donnell et al. 2012) were highly similar. However, the usage of two scales in the analysis made it possible to make more nuanced predictions.

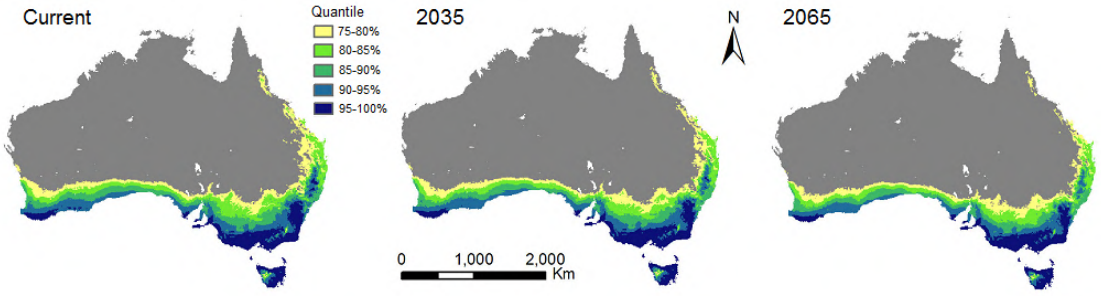

Fig. 20. Maps of Australia showing the location of potential hotspots which represent the combined binary distributions of suitable habitat for 292 naturalized but not yet invasive plant species based on the top 5th, 10th, 15th, 20th and 25th percentiles for three time periods (current, 2035 and 2065) (from Duursma et al. 2013 with changes). The grey region represents areas where the combined suitability across all 292 species is less than the 25th percentile.

The two following examples illustrate the identification of invasion hotspots on smaller geographic scale. Lazzaro et al. (2017) produced, using SDM, a "Potential threat of invasion" map and combined it with the distribution of high conservation value habitats to identify areas of greatest concern. The target area was Tuscan Archipelago National Park, which covers more than half of the Island Elba.

Six species were selected that are considered the most harmful invaders in the Tuscan Archipelago: *Acacia dealbata*, *Agave americana*, *A. altissima*, *Opuntia fius-indica*, *O. pes-caprae* and *Robinia pseudoacacia*. The number of occurrences of the alien species varied from 95 for *A. altissima* to 150 for *A. dealbata*. Predictors included climatic, topographic, vegetation type, and antropogenic variables. The cell size of the maps was 100 x 100 m. The continuous probabilistic output was converted to binary, and the "Potential threat of invasion" was calculated for each grid cell by summing the six species predictions of habitat suitability. In addition, the "Risk of invasion" was calculated. The latter was a product of the "Potential threat of invasion" and a measure of conservation value of the local biota "Habitat density" derived from the map of Natura2000 habitats on Elba Island (Fig. 21). The length of roads per cell was found to be the most important factor in determining the presence of a species. Habitats more at risk of invasion were closer to roads and anthropic habitats. Based on predicted vulnerability to invasion and conservation value, the authors identified coastal habitats as areas of greatest concern.

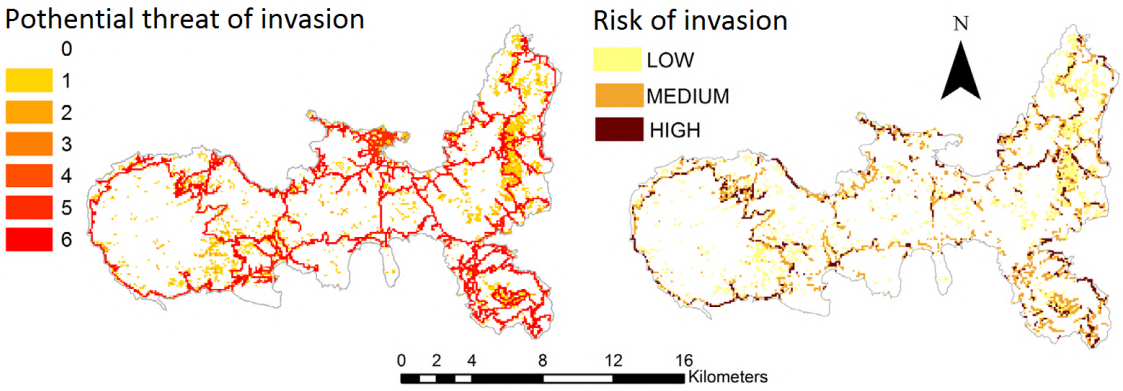

Fig. 21. Predicted maps of threat of invasion obtained as the sum of the potential presence of the six invasive species, and of risk of invasion (areas of conservation concern with three levels of risk) for the Island of Elba (from Lazzaro et al. 2017).

Vorsino et al. (2014) assessed the invasibility of Hawaiian ecosystems through ensembling SDM predictions for top 17 invasive plant species. The authors estimated the current (2013) and future (2100) distribution of invasibility (and its change over time) throughout the Hawaiian Islands, and in relation to the federally designated critical habitats for threatened endemic Hawaiian organisms. The modeling utilized five bioclimatic and two topographic variables with a resolution of 250 m and several SDM algorithms. The produced models were ensembled in *biomod2* program. A suite of 17 ensemble models (one pre species) was used as an "invasibility index" to highlight areas of both actual and potential habitat degradation due to invasive species habitat suitability (Fig. 22).

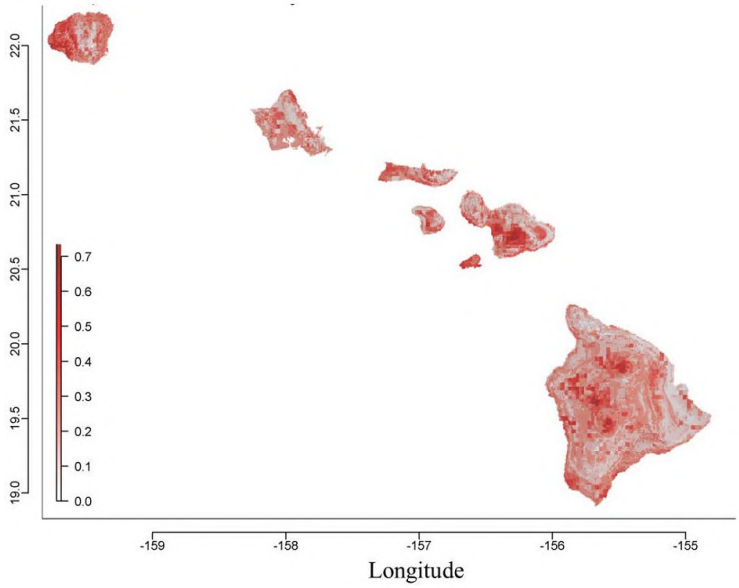

Fig. 22. Map of Hawaii with Additive Invasibility Index combining current and future climate predictions for the invasive species diversity per site.

Application of SDM in Central Asia

As I tried to show in the preceding sections, SDM has a wide spectrum of applications, making it a valuable tool for botanists, foresters, horticulturists, landscape designers, but first of all, conservation biologists. The ability of SDM to predict habitat suitability for species with poorly documented ranges makes it a tool especially suited to regions like Central Asia. As was discussed in Volis (2022), Central Asia is a region where high climatic, topographic and edaphic heterogeneity and specific evolutionary history have created variety of endemic species with narrow habitat specialization and very restricted ranges. Many red-listed Central Asian species are known from only a few or a single location. Any plans for these species recovery must be based on the estimates of their area of occupancy and critical habitat, as well as knowledge of their habitat requirements and potential range. SDM can be used as a tool for getting these estimates. The predicted ranges can then be used for identification of biodiversity and endemism hotspots, and for reserve design.

Let's have a look at the scarce literature on SDM studies performed on Central Asian species. SDM was used to analyze the range and habitat requirements of such animal species having a part of their distribution in Central Asia as reptiles *Varanus griseus* (Malakhov & Chirikova 2018), *Paralaudakia caucasia* (Hosseinian Yousefkhani et al. 2013), *Paralaudakia lehmanni* (Sancholi 2018), mammals *Ursus arctos* (Su et al. 2018), *Otocolobus manul* (Greenspan & Giordano 2021), *Pantera uncia* (Holt et al. 2018; Poyarkov & Rozhnov 2019), birds *Falco cherrug* (Sutton & Puschendorf 2020).

The list of plant species for which SDM was performed is even more modest. SDM was applied to several economically important and ecosystem keystone tree species: two *Haloxylon* species, *H. persicum* and *H. amodendron* (Li et al. 2019), *Pistacia vera* (Malakhov & Islamgulova 2021) and *Juglans regia* (Gaisberger et al. 2020). The first studies applying SDM to threatened Central Asian plant species appeared in 2019. Tojibaev et al (2019) predicted a suitable habitat for the Uzbek endemic *O. bucharica* under both current and expected by 2070 climate. In addition, since *O. acuminata* is edaphically

specialised, growing exclusively on gypsum soil, they produced a map of gypsum soil in Uzbekistan, and overlaid it on the above projected climatic suitability range. This allowed identification of the areas suitable for the species not only climatically and topographically, but also edaphically (Fig. 23).

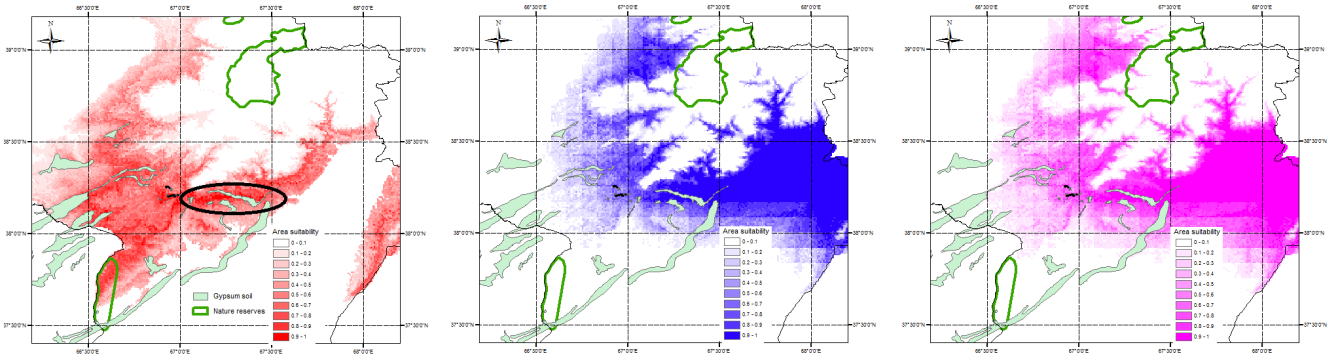

Fig. 23. The predicted suitable species range under current (left) and expected in year 2070 under RCP2.6 (middle) and RCP8.5 (right) scenarios climate. Suitability corresponds to intensity of color. Ellipsoid contour denotes the area where a new nature reserve should be established (from Tojibaev et al. 2019).

In the same year, Wilson et al. (2019) applied SDM to *Malus niedzwetzkyana* to identify climatically suitable regions and potential areas for restoration in southern Kyrgyzstan. They found that the potential species range is considerably greater than the current one (Fig. 24), and many areas of degraded forest can be a subject to restoration using M. niedzwetzkyana and other species characteristic to walnut–fruit forest ecosystems. Then, two studies were published in 2021-2022. The study by Volis and Tojibaev (2022) is described in one of the previous sections. In another, Wilson et al. (2021) undertook SDM to assess suitable habitat for ten Central Asian tulip species (Fig. 25). This work has shown that climate change will have a significant negative impact on the size of the range of all species, including those that are currently widespread, and that regional-level models provide a much better understanding of species' potential range and limitations in PA coverage.

The above four studies show that SDM is gaining popularity in Central Asian plant conservation research, and we can expect the number of such studies to increase rapidly in the coming years. However, in all the above studies the aim was to identify a suitable

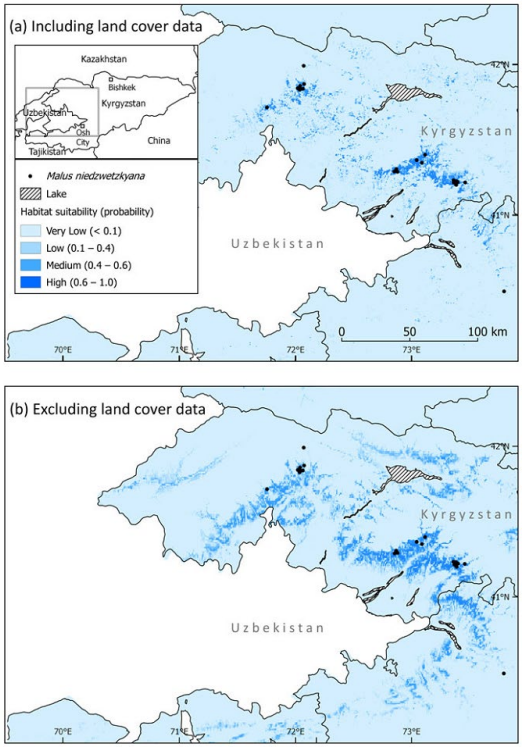

Fig. 24. Predicted suitable habitat for *Malus niedzwetzkyana* in Kyrgyzstan (a) including land cover data and (b) excluding land cover data (from Wilson et al. 2019).

area for a target species; even if SDM was performed for many species, the outcome were separate maps of the species suitable habitat. Diversity maps produced by overlaying (stacking) the predicted species distributions and used for elucidating spatial patterns of species richness and endemism, are still lacking for Central Asia. The procedure involving stacking the individual-species values per cell (pixel) is called stacked species distribution modelling (S-SDM) (Guisan & Rahbek 2011). The prospects for the application of this method in Central Asia can be seen in the following example. I used the occurrence data for 63 endemic Uzbek plant species to produce, using the program "ssdm" (Schmitt et al. 2017), S-SDM maps of species richness and endemism. The species richness maps shown in Fig. 26 were produced with four different SDM algorithms, Classification Trees Analysis (CTA), Artificial Neural Networks (ANN), MAXENT, and Random Forest (RF). The endemism maps (Fig. 27) were produced using two indices: Weighted Endemism Index (WEI) and Corrected Weighted Endemism Index (CWEI). WEI weights each species in a cell by the inverse of its range, and then sums those weights for all species in the cell. A species occurring in a single cell has the maximum weight of 1, while a species occurring in ten cells has a weight of 0.1. When CWEI is employed, an endemism map is constructed by dividing the weighted endemism index by the total count of species in the cell. This index corrects for the species richness effect (i.e. higher scores get cells with higher proportion of range-restricted endemics).

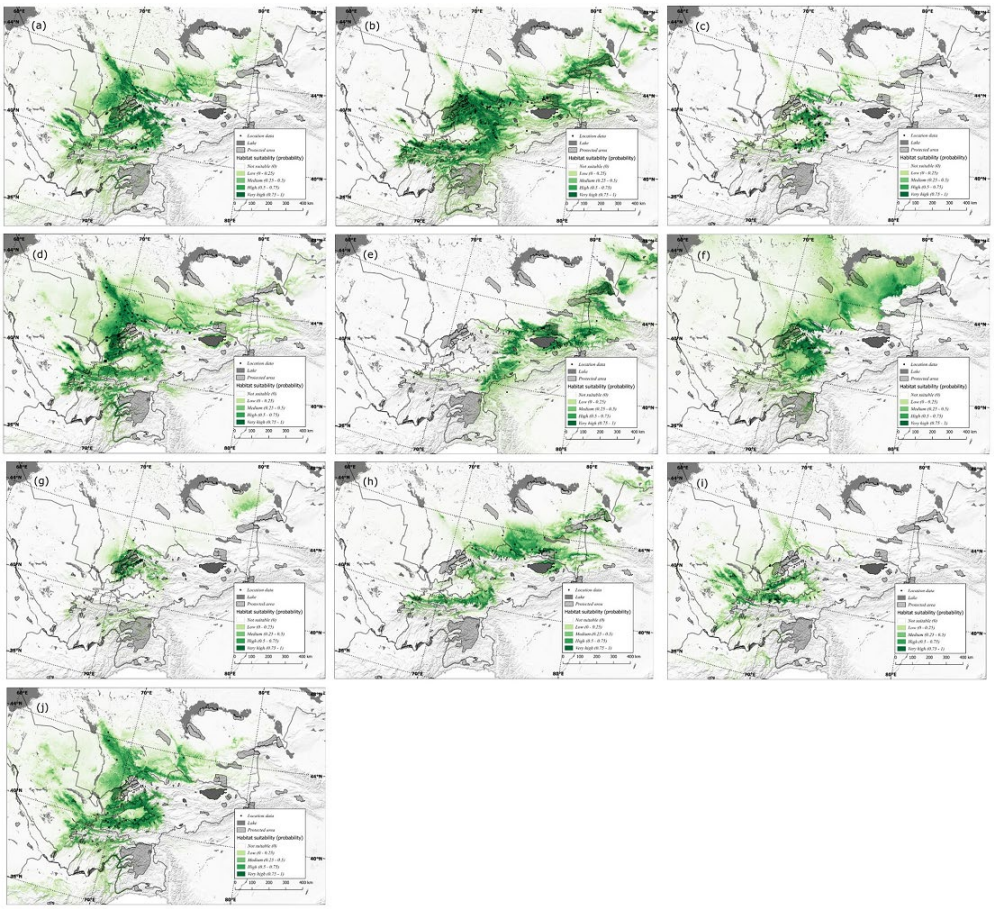

Fig. 25. Predicted suitable habitat for ten Central Asian endemic *Tulipa* species (from Wilson et al. 2021).

As we can see, the geographic patterns of species richness and endemism are highly similar, and also coincide with the conservation priority map produced by Zonation from the occurrence data for 50 critically endangered plant species (Fig. 28. In my view, this is convincing evidence that SDM should become a routinely used tool for conservation planning in Central Asia, with wide spectrum of applications described and discussed in the first part of the paper.

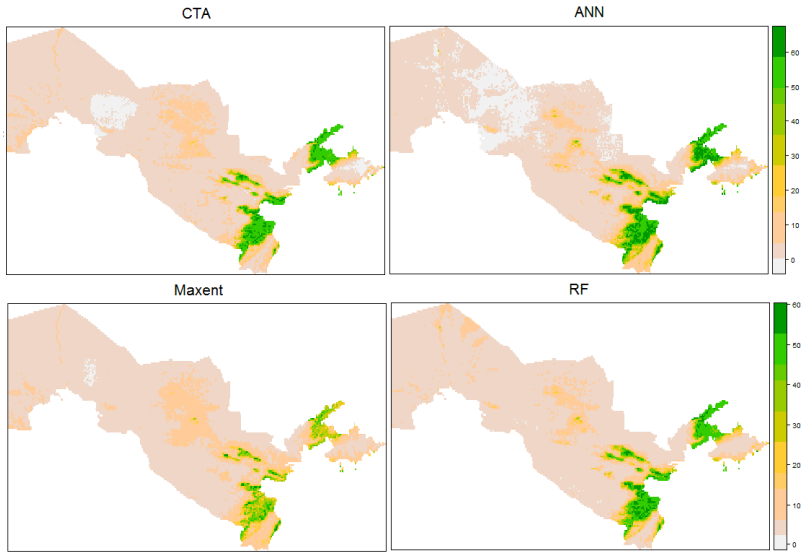

Fig. 26. S-SDM maps of species richness produced from occurrence data for 63 Uzbek endemic plant species by 4 SDM algorithms with default settings

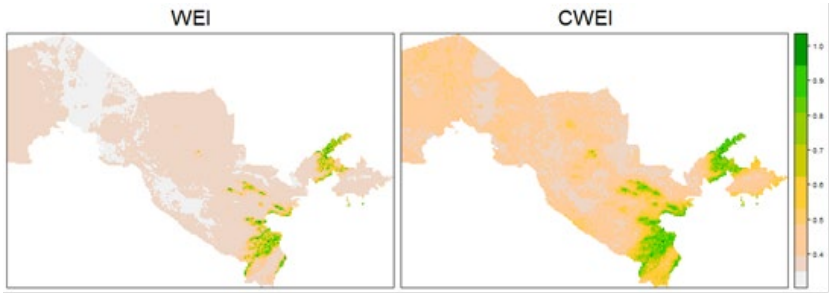

Fig. 27. S-SDM maps of predicted endemism produced from occurrence data for 63 Uzbek endemic plant species using two endemism indices (WEI and CWEI)

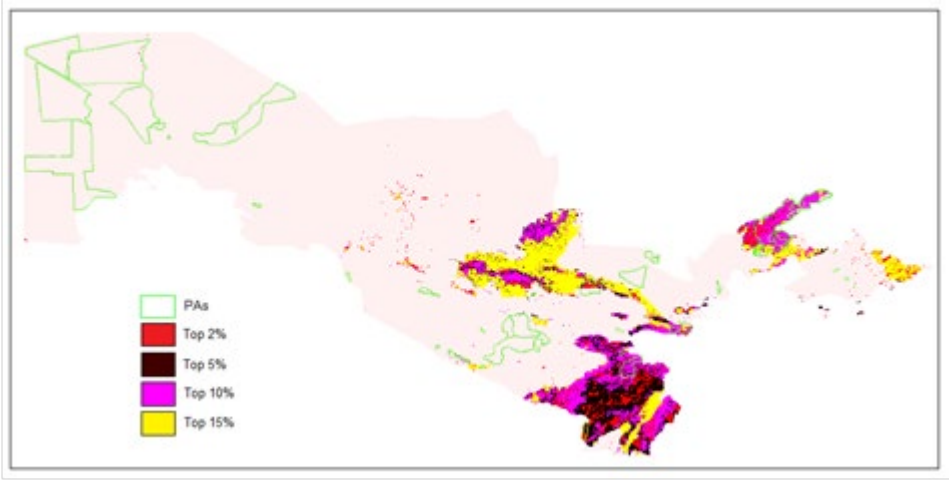

Fig. 28. Spatial distribution of conservation priorities produced from occurrence data for 50 critically endangered Uzbek plant species by Zonation, and the existing in Uzbekistan protected areas (PAs). Nested hierarchical ranking of conservation priorities is shown for four levels: top 2%, 5%, 10% and 15% (from Volis & Tojibaev 2022).

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References

Araujo MB, Cabeza M, Thuiller W, Hannah L, Williams PH (2004) Would climate change drive species out of reserves? An assessment of existing reserve‐selection methods. *Global Change Biology* 10: 1618-1626.

Araujo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33: 1677-1688.

Attorre F, De Sanctis M, Farcomeni A, Guillet A, Scepi E, Vitale M, Pella F, Fasola M (2013) The use of spatial ecological modelling as a tool for improving the assessment of geographic range size of threatened species. *Journal for Nature Conservation* 21: 48-55.

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157: 101-118.

Bachman S, Moat J, Hill AW, De La Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *ZooKeys* 150: 117-126.

Baumgartner JB, Esperón‐Rodríguez M, Beaumont LJ (2018) Identifying in situ climate refugia for plant species. *Ecography* 41: 1850-1863.

Bonebrake TC, Syphard AD, Franklin J, Anderson KE, Akçakaya HR, Mizerek T, Winchell C, Regan HM (2014) Fire management, managed relocation, and land conservation options for long‐lived obligate seeding plants under global changes in climate, urbanization, and fire regime. *Conservation Biology* 28: 1057-1067.

Bourg NA, McShea WJ, Gill DE (2005) Putting a cart before the search: successful habitat prediction for a rare forest herb. *Ecology* 86: 2793-2804.

Bradley BA, Oppenheimer M, Wilcove DS (2009) Climate change and plant invasions: restoration opportunities ahead? *Global Change Biology* 15: 1511-1521.

Brambilla M, Caprio E, Assandri G, Scridel D, Bassi E et al. (2017) A spatially explicit definition of conservation priorities according to population resistance and resilience, species importance and level of threat in a changing climate. *Diversity and Distributions* 23: 727–738.

Breiner FT, Guisan A, Nobis MP, Bergamini A (2017) Including environmental niche information to improve IUCN Red List assessments. *Diversity and Distributions* 23: 484-495.

Cardoso P, Borges PAV, Triantis KA, Ferrández MA, Martín JL (2011) Adapting the IUCN Red List criteria for invertebrates. *Biological Conservation* 144: 2432-2440.

Chape S, Harrison J, Spalding M, Lysenko I (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 443-455.

Choe H, Thorne JH, Hijmans R, Kim J, Kwon H, Seo C (2017) Meta‐corridor solutions for climate‐vulnerable plant species groups in South Korea. *Journal of Applied Ecology* 54: 1742-1754.

Choe H, Thorne JH, Huber PR, Lee D, Quinn JF (2018) Assessing shortfalls and complementary conservation areas for national plant biodiversity in South Korea. *PLoS ONE* 13: e0190754.

Cole KL, Ironside K, Eischeid J, Garfin G, Duffy PB, Toney C (2011) Past and ongoing shifts in Joshua tree distribution

support future modeled range contraction. *Ecological Applications* 21: 137-149.

Conroy GC, Shimizu-Kimura Y, Lamont RW, Ogbourne SM (2019) A multidisciplinary approach to inform assisted migration of the restricted rainforest tree, *Fontainea rostrata*. *PLoS ONE* 14: e0210560.

Costa GC, Nogueira C, Machado RB, Colli GR (2010) Sampling bias and the use of ecological niche modeling in conservation planning: a field evaluation in a biodiversity hotspot. *Biodiversity and Conservation* 19: 883-899.

Crall AW, Jarnevich CS, Panke B, Young N, Renz M, Morisette J (2013) Using habitat suitability models to target invasive plant species surveys. *Ecological Applications* 23: 60-72.

Cuesta F, Peralvo M, Merino-Viteri A, Bustamante M, Baquero F, Freile JF, Muriel P, Torres-Carvajal O (2017) Priority areas for biodiversity conservation in mainland Ecuador. *Neotropical Biodiversity* 3: 93-106.

de Castro Pena JC, Kamino LHY, Rodrigues M, Mariano-Neto E, de Siqueira MF (2014) Assessing the conservation status of species with limited available data and disjunct distribution. *Biological Conservation* 170: 130-136.

de Siqueira MF, Durigan G, de Marco Júnior P, Peterson AT (2009) Something from nothing: using landscape similarity and ecological niche modeling to find rare plant species. *Journal for Nature Conservation* 17: 25-32.

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'amen M, Randin C, Engler R, Pottier J, Pio D, Dubuis A (2017) *ecospat*: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography* 40: 774-787.

Draper D, Marques I, Iriondo JM (2019) Species distribution models with field validation, a key approach for successful selection of receptor sites in conservation translocations. *Global Ecology and Conservation* 19: e00653.

Dumroese RK, Williams MI, Stanturf JA, Clair JBS (2015) Considerations for restoring temperate forests of tomorrow: forest restoration, assisted migration, and bioengineering. *New Forests* 46: 947-964.

Duursma DE, Gallagher RV, Roger E, Hughes L, Downey PO, Leishman MR (2013) Next-generation invaders? Hotspots for naturalised sleeper weeds in Australia under future climates. *PLoS ONE* 8: e84222.

Ferrier S (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? *Systematic Biology* 51: 331-363.

Fiedler PL, Laven RD (1996) Selecting reintroduction sites. In: Falk DA, Millar CI, Olwell M (eds), Restoring Diversity: strategies for reintroduction of endangered plants. Island Press, Washington, DC, pp. 157–170.

Fleishman E, Noss RF, Noon BR (2006) Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators* 6: 543-553.

Fois M, Cuena-Lombrana A, Fenu G, Cogoni D, Bacchetta G (2016) The reliability of conservation status assessments at regional level: past, present and future perspectives on *Gentiana lutea* L. ssp. *lutea* in Sardinia. *Journal for Nature Conservation* 33: 1-9.

Fois M, Fenu G, Lombrana AC, Cogoni D, Bacchetta G (2015) A practical method to speed up the discovery of unknown populations using Species Distribution Models. *Journal for Nature Conservation* 24: 42-48.

Franklin J (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* 19: 474-499.

Franklin J (2009) Mapping species distributions: Spatial inference and predictions. Cambridge University Press, New York.

Gaisberger H, Legay S, Andre C, Loo J, Azimov R, Aaliev S, Bobokalonov F, Mukhsimov N, Kettle C, Vinceti B (2020) Diversity under threat: connecting genetic

diversity and threat mapping to set conservation priorities for *Juglans regia* L. populations in Central Asia. *Frontiers in Ecology and Evolution* 8: 171.

Game ET, Lipsett-Moore G, Saxon E, Peterson N, Sheppard S (2011) Incorporating climate change adaptation into national conservation assessments. *Global Change Biology* 17: 3150-3160.

García A (2006) Using ecological niche modelling to identify diversity hotspots for the herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. *Biological Conservation* 130: 25-46.

Garcia del Barrio JM, Aunon F, Sanchez de Ron D, Alia R (2013) Assessing regional species pools for restoration programs in Spain. *New Forests* 44: 559-576.

Gärdenfors U, Hilton-Taylor C, Mace GM, Rodríguez JP (2001) The application of IUCN Red List criteria at regional levels. *Conservation Biology* 15: 1206-1212.

Gioia P, Pigott JP (2000) Biodiversity assessment: a case study in predicting richness from the potential distributions of plant species in the forests of south-western Australia. *Journal of Biogeography* 27: 1065-1078.

Greenspan E, Giordano AJ (2021) A rangewide distribution model for the Pallas's cat (*Otocolobus manul*): identifying potential new survey regions for an understudied small cat. *Mammalia* 85: 574-587.

Groves CR, Game ET, Anderson MG, Cross MS, Enquist C, Ferdana Z, Girvetz E, Gondor A, Hall KR, Higgins J, Marshall R, Popper K, Schill S, Shafer S (2012) Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation* 21: 1651-1671.

Guillera-Arroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kujala H, Lentini PE, McCarthy MA, Tingley R, Wintle BA (2015) Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography* 24: 276-292.

Guisan A, Rahbek C (2011) SESAM – a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography* 38: 1433-1444.

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecological Letters* 8: 993-1009.

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147-186.

Guo J-L, Yu Y-H, Zhang J-W, Li Z-M, Zhang Y-H, Volis S (2019) Conservation strategy for aquatic plants: endangered *Ottelia acuminata* (Hydrocharitaceae) as a case study. *Biodiversity and Conservation* 28: 1533-1548.

Hannah L, Midgley G, Andelman S, Araujo M, Hughes G, Martinez-Meyer E, Pearson R, Williams P (2007) Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* 5: 131-138.

Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford, UK.

Holt CDS, Nevin OT, Smith D, Convery I (2018) Environmental niche overlap between snow leopard and four prey species in Kazakhstan. *Ecological Informatics* 48: 97-103.

Hosseinian Yousefkhani SS, Ficetola GF, Rastegar-Pouyani N, Ananjeva NB, Rastegar-Pouyani E, Masroor R (2013) Environmental suitability and distribution of the Caucasian Rock Agama, *Paralaudakia caucasia* (Sauria: Agamidae) in western and central Asia. *Asian Herpetological Research* 4: 207-213.

Huenneke LF (1991) Ecological implications of genetic variation in plant populations. In: Falk DA, Holsinger KE (eds), Genetics and Conservation of Rare Plants. Oxford University Press, New York, pp. 31-44.

Hutchinson G (1957) Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology. pp. 415-427.

Hutchinson GE (1978) An introduction to population ecology. Yale University Press, New Haven.

Ibanez I, Silander Jr JA, Allen JM, Treanor SA, Wilson A (2009) Identifying hotspots for plant invasions and forecasting focal points of further spread. *Journal of Applied Ecology* 46: 1219-1228.

IUCN (2001) UCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission, Gland, Switzerland and Cambridge, UK.

IUCN (2016) Guidelines for using the IUCN red list categories and criteria version 12. Data available at. http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

IUCN (2017) IUCN Standards and Petitions Subcommittee. Guidelines for using the IUCN RedList categories and criteria. IUCN.

Jarvis A, Williams K, Williams D, Guarino L, Caballero PJ, Mottram G (2005) Use of GIS for optimizing a collecting mission for a rare wild pepper (*Capsicum flexuosum* Sendtn.) in Paraguay. *Genetic Resources and Crop Evolution* 52: 671-682.

Jiménez-Alfaro B, Draper D, Nogués-Bravo D (2012) Modeling the potential area of occupancy at fine resolution may reduce uncertainty in species range estimates. *Biological Conservation* 147: 190-196.

Jiménez-Valverde A, Lobo JM, Hortal J (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions* 14: 885-890.

Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. *Biological Invasions* 13: 2785-2797.

Kearney M (2006) Habitat, environment and niche: what are we modelling? *Oikos* 115: 186-191.

Keppel G, Mokany K, Wardell-Johnson GW, Phillips BL, Welbergen JA, Reside AE (2015) The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment* 13: 106-112.

Klorvuttimontara S, McClean CJ, Hill JK (2011) Evaluating the effectiveness of Protected Areas for conserving tropical forest butterflies of Thailand. *Biological Conservation* 144: 2534-2540.

Koch R, Almeida-Cortez JS, Kleinschmit B (2017) Revealing areas of high nature conservation importance in a seasonally dry tropical forest in Brazil: Combination of modelled plant diversity hot spots and threat patterns. *Journal for Nature Conservation* 35: 24-39.

Krause C, Pennington D (2012) Strategic decisions in conservation: using species distribution modeling to match ecological requirements to available habitat. In: Maschinski J, Haskins KE (eds), Plant reintroduction in a changing climate: Promises and perils. Island Press, Washington, DC, pp. 131-153.

Kremen C, Cameron A, Moilanen A, Phillips SJ, Thomas CD, Beentje H, Dransfield J, Fisher BL, Glaw F, Good TC (2008) Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* 320: 222-226.

Lannuzel G, Balmot J, Dubos N, Thibault M, Fogliani B (2021) High-resolution topographic variables accurately predict the distribution of rare plant species for conservation area selection in a narrow-endemism hotspot in New Caledonia. *Biodiversity and Conservation* 30: 963-990.

Lazzaro L, Viciani D, Dell'Olmo L, Foggi B (2017) Predicting risk of invasion in a Mediterranean island using niche modelling and valuable biota. *Plant Biosystems* 151: 361-370.

Lessmann J, Munoz J, Bonaccorso E (2014) Maximizing species conservation in continental Ecuador: a case of systematic conservation planning for biodiverse regions. *Ecology and Evolution* 4: 2410-2422.

Li J, Chang H, Liu T, Zhang C (2019) The potential geographical distribution of *Haloxylon* across Central Asia under

climate change in the 21st century. *Agricultural and Forest Meteorology* 275: 243-254.

Lodge DM, Simonin PW, Burgiel SW, Keller RP, Bossenbroek JM, Jerde CL, Kramer AM, Rutherford ES, Barnes MA, Wittmann ME (2016) Risk analysis and bioeconomics of invasive species to inform policy and management. *Annual Review of Environment and Resources* 41: 453-488.

Lomba A, Pellissier L, Randin C, Vicente J, Moreira F, Honrado J, Guisan A (2010) Overcoming the rare species modelling paradox: a novel hierarchical framework applied to an Iberian endemic plant. *Biological Conservation* 143: 2647-2657.

Malakhov D, Islamgulova A (2021) The ecological niche of *Pistacia Vera* L.(Anacardiaceae) in Central Asia: A comprehensive tool for agromeliorative planning. *Biosis: Biological Systems* 2: 209-216.

Malakhov DV, Chirikova MA (2018) Species distribution model of *Varanus griseus caspius* (Eichwald, 1831) in Central Asia: an insight to the species' biology. *Russian Journal of Herpetology* 25: 195-206.

Manish K, Pandit MK (2019) Identifying conservation priorities for plant species in the Himalaya in current and future climates: A case study from Sikkim Himalaya, India. *Biological Conservation* 233: 176-184.

Marcer A, Sáez L, Molowny-Horas R, Pons X, Pino J (2013) Using species distribution modelling to disentangle realised versus potential distributions for rare species conservation. *Biological Conservation* 166: 221-230.

McCune JL (2016) Species distribution models predict rare species occurrences despite significant effects of landscape context. *Journal of Applied Ecology* 53: 1871-1879.

Menon S, Choudhury BI, Khan ML, Peterson AT (2010) Ecological niche modeling and local knowledge predict new populations of *Gymnocladus assamicus* a critically endangered tree species. *Endangered Species Research* 11: 175-181.

Moat J, Bachman S (2017) GeoCAT Geospatial Conservation Assessment Tool. Retrieved from http://geocat.kew.org/.

Muñoz-Rodríguez P, Munt DD, Saiz JCM (2016) Global strategy for plant conservation: inadequate in situ conservation of threatened flora in Spain. *Israel Journal of Plant Sciences* 63: 297-308.

Newbold T, Gilbert F, Zalat S, El‐Gabbas A, Reader T (2009) Climate-based models of spatial patterns of species richness in Egypt's butterfly and mammal fauna. *Journal of Biogeography* 36: 2085-2095.

O'Donnell J, Gallagher RV, Wilson PD, Downey PO, Hughes L, Leishman MR (2012) Invasion hotspots for non-native plants in Australia under current and future climates. *Global Change Biology* 18: 617-629.

Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology* 78: 419-433.

Peterson AT, Vieglais DA (2001) Predicting Species Invasions Using Ecological Niche Modeling: New Approaches from Bioinformatics Attack a Pressing Problem: A new approach to ecological niche modeling, based on new tools drawn from biodiversity informatics, is applied to the challenge of predicting potential species' invasions. *BioScience* 51: 363-371.

Powell M, Accad A, Shapcott A (2005) Geographic information system (GIS) predictions of past, present habitat distribution and areas for re-introduction of the endangered subtropical rainforest shrub *Triunia robusta* (Proteaceae) from south-east Queensland Australia. *Biological Conservation* 123: 165-175.

Poyarkov AD, Rozhnov VV (2019) Potential habitat of snow leopard (*Panthera uncia*, Felinae) in south Siberia and adjacent territories based on the maximum entropy distribution model. *Зоологический журнал* 98: 332-342.

Pulliam HR (1988) Sources, sinks, and population regulation. *American Naturalist* 132: 652-661.

Pulliam HR (2000) On the relationship between niche and distribution. *Ecology Letters* 3: 349-361.

Rabinowitz D (1981) Seven forms of rarity. In: Synge H (ed.), The biological aspects of rare plant conservation, Wiley, Chichester, pp. 205-217.

Renteria JL, Rouget M, Visser V (2017) Rapid prioritization of alien plants for eradication based on climatic suitability and eradication feasibility. *Austral Ecology* 42: 995-1005.

Rondinini C, Wilson KA, Boitani L, Grantham H, Possingham HP (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters* 9: 1136-1145.

Rovzar C, Gillespie TW, Kawelo K (2016) Landscape to site variations in species distribution models for endangered plants. *Forest Ecology and Management* 369: 20–28.

Sáenz-Romero C, Rehfeldt GE, Duval P, Lindig-Cisneros RA (2012) *Abies religiosa* habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico. *Forest Ecology and Management* 275: 98-106.

Sancholi N (2018) Effects of climate change on *Paralaudakia lehmanni* (Nicolsky, 1896) (Reptilia: Agamidae) in Central Asia. *Contemporary Problems of Ecology* 11: 682-686.

Särkinen T, Gonzáles P, Knapp S (2013) Distribution models and species discovery: the story of a new *Solanum* species from the Peruvian Andes. *PhytoKeys* 31: 1-20.

Schmitt S, Pouteau R, Justeau D, de Boissieu F, Birnbaum P (2017) *ssdm*: An r package to predict distribution of species richness and composition based on stacked species distribution models. *Methods in Ecology and Evolution* 8: 1795-1803.

Sérgio C, Figueira R, Draper D, Menezes R, Sousa AJ (2007) Modelling bryophyte distribution based on ecological information for extent of occurrence assessment. *Biological Conservation* 135: 341-351.

Shapcott A, Powell M (2011) Demographic structure, genetic diversity and habitat distribution of the endangered, Australian rainforest tree *Macadamia jansenii* help facilitate an introduction program. *Australian Journal of Botany* 59: 215-225.

Shoo LP, Storlie C, Vanderwal J, Little J, Williams SE (2011) Targeted protection and restoration to conserve tropical biodiversity in a warming world. *Global Change Biology* 17: 186-193.

Siles G, Alcantara JM, Rey PJ, Bastida JM (2010) Defining a target map of native species assemblages for restoration. *Restoration Ecology* 18: 439-448.

Soberon J (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10: 1115–1123.

Soberon J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2: 1–10.

Spiers JA, Oatham MP, Rostant LV, Farrell AD (2018) Applying species distribution modelling to improving conservation based decisions: a gap analysis of Trinidad and Tobago's endemic vascular plants. *Biodiversity and Conservation* 27: 2931-2949.

Su J, Aryal A, Hegab IM, Shrestha UB, Coogan SCP, Sathyakumar S, Dalannast M, Dou Z, Suo Y, Dabu X (2018) Decreasing brown bear (*Ursus arctos*) habitat due to climate change in Central Asia and the Asian Highlands. *Ecology and Evolution* 8: 11887-11899.

Sutton LJ, Puschendorf R (2020) Climatic niche of the Saker Falcon *Falco cherrug*: predicted new areas to direct population surveys in Central Asia. *Ibis* 162: 27-41.

Swart C, Donaldson J, Barker N (2018) Predicting the distribution of *Encephalartos latifrons*, a critically endangered cycad in South Africa. *Biodiversity and Conservation* 27: 1961-1980.

Taylor C, Cadenhead N, Lindenmayer DB, Wintle BA (2017) Improving the design of

a conservation reserve for a critically endangered species. *PLoS ONE* 12: e0169629.

Thorn JS, Nijman V, Smith D, Nekaris KAI (2009) Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). *Diversity and Distributions* 15: 289-298.

Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M (2005a) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11: 2234-2250.

Tojibaev K, Beshko N, Volis S (2019) Translocation of *Otostegia bucharica*, a highly threatened narrowly distributed relict shrub. *Plant Diversity* 41: 105-108.

Volis S (2022) Conservation-oriented restoration and its application to Central Asia. *Plant Diversity of Central Asia* 1: 1-19.

Volis S, Tojibaev K (2021) Defining critical habitat for plant species with poor occurrence knowledge and identification of critical habitat networks. *Biodiversity and Conservation* 30: 3603-3611.

Vorsino AE, Fortini LB, Amidon FA, Miller SE, Jacobi JD, Price JP, Koob GA (2014) Modeling Hawaiian ecosystem degradation due to invasive plants under current and future climates. *PLoS ONE* 9: e95427.

Wang H-H, Wonkka CL, Treglia ML, Grant WE, Smeins FE, Rogers WE (2015) Species distribution modelling for conservation of an endangered endemic orchid. *Aob Plants* 7: plv039.

Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications* 21: 335-342.

Williams JN, Seo C, Thorne J, Nelson JK, Erwin S, O'Brien JM, Schwartz MW (2009) Using species distribution models to predict new occurrences for rare plants. *Diversity and Distributions* 15: 565-576.

Wilson B, Dolotbakov A, Burgess BJ, Clubbe C, Lazkov G, Shalpykov K, Ganybaeva M, Sultangaziev O, Brockington SF (2021) Central Asian wild tulip conservation requires a regional approach, especially in the face of climate change. *Biodiversity and Conservation* 30: 1705-1730.

Wilson B, Mills M, Kulikov M, Clubbe C (2019) The future of walnut-fruit forests in Kyrgyzstan and the status of the iconic Endangered apple *Malus niedzwetzkyana*. *Oryx* 53: 415-423.

Wittenberg R, Cock MJ (2005) Best practices for the prevention and management of invasive alien species. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (eds), Invasive alien species. A new synthesis. Island Press, Wahington DC, pp. 209–232.