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Prioritizing forest patches to enhance habitat restoration and connectivity for the endangered saproxylic beetle *Rosalia alpina* (Coleoptera, Cerambycidae): a modelling approach.

Priorización de parches forestales con el fin de favorecer la restauración del hábitat y la conectividad del escarabajo saproxílico *Rosalia alpina* (Coleoptera, Cerambycidae): un enfoque de modelización.

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Abstract

The cerambycid beetle *Rosalia alpina* is associated with temperate, broadleaved (mainly beech) forests containing dead or decaying wood. This species is protected under the Habitats Directive of the European Union. Given its narrow ecological niche and limited dispersal abilities, habitat fragmentation is a conservation concern for populations of *R. alpina*. In order to maximise the effectiveness of habitat restoration, a scientifically sound procedure for patch selection is needed. In Gipuzkoa (N Spain), we used Light Detection and Ranging (LiDAR) images to search for 20x20-m cells matching the parameterisation of a predictive and local habitat model for *R. alpina* at the tree level. The cells selected under quantitative criteria were clustered to identify potential habitat patches. Conefor Sensinode software was used to estimate the importance of each of those patches in terms of the connectivity

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of the population, based on dispersal distances of *R. alpina* and the probabilities of dispersing events among patches. We identified 380 potential habitat patches, mostly in the south-eastern sector of the study area, which were classified into "core areas" and "connecting areas". The performance of the model was tested in the field (61% of correct assignations), although the actual occurrence of *R. alpina* within the habitat patches should be assessed in the future. This model represents a step forward in guiding the cost-effective implementation of conservation activities, through a strict preservation of the current core habitat patches and an increase in the size of connecting patches. Therefore, we show that connectivity models combining remote sensing data and local habitat selection can be an aid in conservation planning and restoration actions, probably outperforming less efficient strategies, such as random or expert selection.

Key words: Beetle, fragmentation, conservation, beech, *Fagus sylvatica*.

Resumen

El escarabajo cerambícido *Rosalia alpina* está asociado a los bosques templados de frondosas (principalmente hayas) que albergan madera muerta o en descomposición. La especie está protegida bajo la Directiva de Hábitats de la Unión Europea. Dado su estrecho nicho ecológico y su limitada capacidad de dispersión, la fragmentación de su hábitat es un problema de conservación para las poblaciones de *R. alpina*. Para maximizar la efectividad de la restauración del hábitat, se necesita un procedimiento científicamente sólido para la selección de parches forestales sobre los que intervenir. En Gipuzkoa (norte de España) utilizamos imágenes LiDAR para buscar celdas de 20x20 m que se ajustaran a la parametrización de un modelo predictivo local de hábitat para *R. alpina* a nivel de árbol. Las celdas seleccionadas bajo criterios cuantitativos fueron agrupadas para identificar parches de hábitat potencial. Se utilizó el software Conefor Sensinode para estimar la importancia de cada uno de estos parches en términos de conectividad para la población, con base en las distancias de dispersión de *R. alpina* y la probabilidad de eventos de dispersión entre parches. Se identificaron 380 parches de hábitat potencial, mayoritariamente en el sector sureste del área de estudio, que fueron clasificados como "áreas centrales" o "áreas de conexión". La ejecutoria del modelo fue testada en campo (61 % de asignaciones correctas), si bien la presencia real de *R. alpina* en los parches de hábitat debería ser confirmada en el futuro. Este modelo constituye un avance para guiar la implementación de actividades de conservación de manera eficiente, mediante la protección estricta de "áreas centrales" y el incremento del tamaño de las "áreas de conexión". Por lo tanto, mostramos que los modelos de conectividad que combinan datos de detección remota y selección local del hábitat pueden asistir en la planificación de la conservación y en las acciones de restauración específicas, seguramente mejorando los resultados de estrategias menos eficientes, como la selección al azar o basada en criterio experto.

Palabras clave: Escarabajo, fragmentación, conservación, haya, *Fagus sylvatica*.

Laburpena

Rosalia alpina kakalardo cerambicidoa atxikita dago egur hila edota deskonposizioan duten baso hostozabal epeletara (batik bat pagadiak). Espeziea Europar Batasuneko Habitat Arteztarauak babesturik dago. Txoko ekologiko mugatua izateagatik eta dispertsiorako ahalmen murritza, habitataren zatiketa kontserbazio arazo handia da *R. alpina* populazioentzat. Habitat berreskurapena ahalik eta eraginkorrena izan dadin beharrezkoak dira zientzia prozedura sendoak, esku hartuko den baso orbain egokienak aukeratzeko. Gipuzkoan (Espainia iparraldean) LiDAR irudiak erabili ditugu 20x20 m-ko zelden bidez *R.alpina*-ren habitataren modelo prediktibo lokalera doitzeko, zuhaitz mailan. Irizpide kuantitatiboen bidez aukeratutako zeldak multzoka bildu dira, habitat potentzialen orbainak antzemateko. Conefor Sensinode softwarea erabili da orbain bakoitzaren garrantzia estimatzeko populazioaren konektagarritasunaren aldetik, *R. alpina*-ren dispertsio distantzian oinarrituz eta orbainen arteko dispertsio aukeren probabilitatea lortzeko. Habitat potentzialeko 380 orbain identifikatu dira, gehienbat ikerketa arearen hego-ekialdeko sektorean, sailkaturik “gune zentralak” eta “konexio gune” eran. Exekuziorako modeloa ingurune naturalean probatu da (%61 antzemate zuzen), baina *R.alpina*-ren presentzia erreala habitateko orbainetan egiaztatu egin beharko litzateke etorkizunean. Modelo hau aurrerapausoa da kontserbazio ekintzak modu eraginkorrean garatzeko, “gune zentralen” babes zorrotza bultzatuz eta “konexio guneen” tamaina areagotuz. Horrenbestez, erakusten dugu konektagarritasun urrutiko detekzioko datuak eta habitaten selekzio lokala uztartzen duten modeloek errestaurazio espezifikoko ekintzetan eta kontserbazio plangintzan lagundu dezaketela, ziurrenik eraginkortasun baxuagoko estrategien emaitza hobetuz, kasurako, zoriz eginiko aukeraketa edota adituen iritzietan oinarrituta.

Gako hitzak: kakalardoa, zatiketa, kontserbazioa, pagoa, *Fagus sylvatica*.

Introduction

Connectivity is a landscape feature that facilitates the movements of organisms and genetic flow (Taylor *et al*., 1993). It allows recovery from population decline, increase in genetic diversity, long-term persistence and adaptation to climate change and habitat fragmentation (McRae *et al.*, 2012). Functional connectivity depends both on the spatial configuration of the landscape and on the dispersal ability of the focal species. For instance, the same forest landscape can be perceived as connected to a species with high mobility, but as fragmented to a different species showing more restricted movements (Baguette and Van Dyck, 2007).

Poor connectivity and isolation of populations have been identified as key factors to the conservation of animal species with low dispersal ability (Thomas, 2000). Therefore, restoration of connectivity is a major concern in conservation practice. However, identifying critical areas for the connectivity of a target population is not straightforward. It requires data on the distribution and demography of related (meta) populations, on the structural and spatial configuration of the landscape, and on the mechanisms that drive individuals to move across that landscape (Hanski, 1998). In many practical contexts, this kind of data is not readily available, so it is necessary to use remote sensing (Corbane *et al*., 2015) and modelling techniques, that provide spatially explicit patterns to design mitigation interventions and to address the lack of connectivity (Jordán *et al.*, 2003; Kajtoch *et al.*, 2014). Currently, this is the only feasible approach to many conservation problems, despite debates over the reliability and applicability of modelling in the practical management of ecosystems.

Saproxylic beetles form a functional group of insects that depend on deadwood. Forest patches with mature trees and decaying substrates harbour a high diversity of saproxylics (Grove, 2002; Lachat *et al.*, 2012; Seibold *et al.*, 2015). Many species and the whole community are good examples of occurrence constrained by habitat fragmentation (Bouget *et al.*, 2014; Jeppsson and Forslund, 2014; Janssen *et al.*, 2016), lack of high-resolution distribution knowledge (Buse *et al.*, 2007) and an "active management/reserve-designation" approach to conservation (D'Amen *et al.*, 2013; Sebek *et al.*, 2013; Gran and Götmark, 2019; Karpi ski *et al.*, 2021). Although various European LIFE projects have targeted conservation of saproxylic beetle communities (European Commission, 2012), initiatives explicitly aimed at increasing functional connectivity for this group are rare in Europe, but have been recently demanded (Houston *et al.*, 2020). Single species systematic conservation planning has seldom been applied, as opposed to multi-species or biodiversity planning (Mizsei *et al.*, 2021).

Rosalia alpina (Linnaeus 1758) is a cerambycid saproxylic beetle, classified as "vulnerable" by the IUCN Red List (World Conservation Monitoring Centre, 1996) and as "least concern" at European level (Horák *et al*., 2010). It is included in annexes II and IV of Directive 92/43/CEE. Its habitat consists of Atlantic and continental broadleaved woodlands (beech *Fagus sylvatica* forests in particular) with veteran trees (Cizek *et al.*, 2009; Drag *et al.*, 2018). The long-term reduction and fragmentation of these woodlands, due mainly to transformation into agriculture fields, have driven the current species geographic distribution in Europe and the Iberian Peninsula, with extensive gaps and remnant populations in mountain ranges (Nieto and Alexander, 2010; Viñolas and Vives, 2012; Bosso *et al.*, 2013). Besides, intensive forestry techniques and the removal of dead wood have caused detrimental effects on the suitability of the existing forest habitats, leading to decline of populations (Nieto and Alexander, 2010). Because of the current dominance of regenerating woodlands and commercial plantations at the landscape level over the European range of *R. alpina*, the isolation of habitat patches harbouring mature trees and dead wood, and the low proportion of observed long-distance (>0,5 km) dispersal movements (Gatter, 1997; Drag *et al.*, 2011), connectivity is a relevant conservation concern for the species (Duelli and Wermelinger, 2005; Drag *et al.*, 2011; Viñolas and Vives, 2012). Therefore, restoring habitat cores and/or connecting areas is a key issue to support gene flow across the landscape (Bosso *et al.*, 2013), but practitioners face the challenge of selecting the most adequate locations and forest patches to maximise the effectiveness of such strategy.

The identification of forest patches with suitable microhabitats (i.e. individual trees large enough to maintain tree-related microhabitats; Kozák *et al*., 2023) for *R. alpina*, in the absence of high resolution and systematic field data on spatial distribution, requires the development of robust probabilistic models (Jansson *et al.*, 2009; Bosso *et al*., 2017) based, if possible, on local knowledge of the species ecology (Russo *et al.*, 2010). An alternative strategy, based on the broad selection of corridors among locations with known occurrence of the species, is not readily applicable in study areas -like ours, see below-, where the available occurrence data has not been systematically collected (i.e., there are probably pseudo-absences) at the spatial scale which is relevant for practitioners involved in actual management (i.e., the surface of legally classified forests or *montes de utilidad pública*, for which compulsory action plans are drafted and implemented). Available records for *R. alpina* in the study area are concentrated in natural parks, where opportunistic observations and some studies focused on saproxylic beetles have been carried out (Castro and Fernández, 2018); e. g., only 8 georeferenced records are retrieved from the Global Biodiversity Information Facility in Gipuzkoa (checklist dataset https://doi.org/10.15468/39omei accessed via GBIF.org on 2023-08-08). The knowledge on the distribution of the species is thus biased to sites which have been sampled and shows low resolution. Classified forests in Gipuzkoa are relatively small on average ($\overline{\chi}$= 93.9 ha, s=294.1, n=311). Finally, corridors designed at coarse scales are rarely applied in real conservation due to practical problems (Boitani *et al*., 2007; Keeley *et al*., 2018), and this is the case in the study area, where ecological corridors targeting an ideal "forest species" were proposed 20 years ago (Gurrutxaga *et al*., 2010) but to date no restorations have taken place.

Here, we use a modelling approach to identify priority areas for the conservation of a regional population of *R. alpina*. The study had the following specific objectives: (1) to identify forest patches holding adequate microhabitats for *R. alpina* at a spatial resolution that is useful for forest planners, managers and practitioners (1:10,000 scale); (2) to identify core patches ("nodes" in terms of connectivity) for *R. alpina*, potentially receiving immigrants or emitting dispersing individuals; and (3) to identify connecting patches ("links" or "stepping-stones") that would support dispersal between nodes in *R. alpina* populations. A preliminary version of this paper was presented at the 6th Spanish Forestry Conference (Fernández-García *et al*., 2013).

Material and methods

Study area

The study area was the province of Gipuzkoa (Basque Country, northern Spain). It comprises 1,978 km^2 and is located in the Atlantic biogeographic region of Europe. Climate is temperate and humid to hyperhumid (c. 2,000 mm of annual rainfall). Although it is densely populated and urbanized in the coastal fringe and in low-altitude valleys, it has also mountain ranges (up to c. 1,550 m asl) where woodland coverage is dominant. Overall, 51.9 % of the province is covered by forest, and about 51.6 % of this surface consists of coniferous commercial plantations (mostly Monterrey pine *Pinus radiata*, larch *Larix* spp., Douglas fir *Pseudotsuga menziessi* and Corsican pine *P. nigra salzmannii*). Beech forest surface reaches 15,315 ha, scattered mainly in the southern and eastern districts of the province (Dirección General de Desarrollo Rural y Política Forestal, 2013). *R. alpina* occurrence in Gipuzkoa is associated to beech forests at mountain ranges (Castro and Fernández, 2018).

Habitat selection model

First, we applied two predictive models of *R. alpina* habitat selection at the tree level, previously published for Gipuzkoa by Castro *et al.* (2012) and Castro and Fernández (2016), using binary logistic regression. The model based on the occurrence of fresh emergence holes (i.e. indicating reproduction) showed that the effective development of the larvae preferably takes place in standing beech trees with dead parts, located inside or at the edges of clearings, exposed to direct, regular sunlight and sheltered from humid winds. The model based on the occurrence of adults suggested that they preferred dead, standing or fallen beeches and large clearings with no preferred orientation (see Castro and Fernández, 2016 for details on both models). Following quantitative criteria and thresholds suggested by Castro *et al.* (2012), the ecological niche of *R. alpina* in Gipuzkoa at the tree level was parameterised by applying five sequential conditions: (1) beech, (2) dead standing tree, (3) tree diameter at 1.30 m >50 cm, (4) dry exposure (other than N-NE-NW-W), and (5) tree inside of or at the edge of a clearing >75 m^2.

Identification of habitat patches

The following available cartographic tools were used: (1) a vegetation map of the National Forest Inventory at scale 1:10,000 (Villanueva, 2009); (2) a map of exposures derived from a digital elevation model, built using a raster dataset with a 25x25-m pixel size (Gobierno Vasco, 2001) and a multiband Light Detection and Ranging (LiDAR) image derived from a flight conducted in 2012, with a pixel size of 20x20-m (Diputación Foral de Gipuzkoa, 2013). We generated a mask with the features "tree species" (restricted to beech), "exposure" and "tree density". To address the differences in scale and overlay, we added a 30 m buffer to the resulting forest patches, and then pixels with total or partial adequate exposure were selected.

Furthermore, a point GIS layer of dead or dying beeches with normal diameter (DBH) >50 cm inventoried in the field was used to produce the model. This layer comprised 63 trees, occupying 56 pixels (20x20 m) distributed throughout the whole study area. A supervised classification of the LiDAR image was performed by the spline interpolation method, restricted to three standard deviations from the mean of the original set of 56 20x20 m pixels. As a result, a total of 5,141 pixels were initially classified (classification 1). Subsequently, a field survey in representative areas was conducted to assess the accuracy of this classification. In total, 64 correct and 145 incorrect pixels were assessed. The pixels correctly classified in the field visits were divided into 11 independent subgroups according to their location and proximity, and a new supervised classification of the LiDAR image was performed by the spline interpolation method at two standard deviations from the means of each of the 11 subgroups (classification 2). In addition, a supervised classification of the original LiDAR image was obtained at two standard deviations from the mean of the 145 pixels that were incorrectly classified (classification 3). Finally, the pixels in classification 2 that did not coincide with classification 3 were accepted into the model. The result consisted of 3,062 pixels that indicated dead or decaying beeches, fitting the topographic, physiognomic, and structural conditions described above.

Once the LiDAR image was classified, we assessed the reliability of the modelling through the confusion matrix and the Kappa estimator. Field verification was conducted for 5% of the pixels, which were randomly chosen, noting that 60.8% included dead or decaying beeches in adequate exposures, and were located inside or at the edge of a clearing. This level of accuracy was considered sufficient to address the study objectives.

Assessment and prioritisation of patches

We used Conefor Sensinode 2.5.8, a software that ranks habitat patches based on their importance for connectivity. The software includes a graphing theoretical algorithm that has been widely and successfully applied in Landscape Ecology research (Urban and Keitt, 2001; Pascual-Hortal and Saura, 2006a, b). Graphs are mathematical structures composed of nodes and links that contain descriptive attributes: area or quality of habitat in the case of nodes and probability of dispersion between two nodes through the link, estimated from Euclidean or functional distances. Conefor Sensinode generates indices that integrate the intrinsic characteristics of the nodes and the topological relationships among them.

One of the indices is Equivalent Connected Area (ECA), which estimates the overall degree of connectivity of a given landscape. It is defined as the surface of a hypothetical continuous habitat patch (therefore fully connected, regardless of its form), that would match the same connectivity probability assessed from the set of patches under study (Saura and Rubio, 2010; Saura *et al.*, 2011a). ECA is calculated using the following expression:

$$ECA=\sqrt{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i \cdot a_j \cdot p^*_{ij}}$$

where a_i and a_j are the areas of patches i and j. ECA has surface units, which facilitates its interpretation. Its value will never be smaller than the area of the largest existing patch in the set under study, and it will coincide with the total habitat area when there is a single patch. Even when several differentiated patches exist, the probability of moving through the available links is maximum for all tessellation edge pairs (p^*_{ij}=1). The global connectivity of the population in the study area is expressed by the relationship between ECA and the total area of available habitat, considering the sum of the surface of the pixels identified by the modelling procedure.

The Probability of Connectivity (PC) index describes the probability of direct dispersion between each pair of nodes and is sensitive to changes that may affect the connectivity and availability of habitat (Saura and Pascual-Hortal, 2007). PC ranges from 0 to 1 and is defined as the probability that two organisms, randomly situated in the landscape, are found in nodes that are interconnected. Its mathematical expression is as follows:

$$PC=\frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j \cdot p^*_{ij}}{A_L^2}=\frac{PCnum}{A_L^2}$$

where n is the number of nodes in the landscape; a_i and a_j are attributes of nodes i and j (surface, quality, etc.); A_L is the maximum value of the attribute of the landscape; and p^*_{ij} is the maximum probability product between nodes i and j. The hierarchy of landscape elements by their contribution to the availability and connectivity of the entire habitat was obtained from the percentage of change of PC (dPC_k), which is generated by removing each k element of the landscape (Keitt *et al.*, 1997; Urban and Keitt, 2001; Saura and Pascual-Hortal, 2007):

$$dPC_k = 100\ \frac{PC_{ini} - PC_{sin}}{PC_{ini}}$$

The pixels accepted after the modelling were grouped into polygons if the euclidean distance between them, calculated with ArcGIS 10.0, was ≤150 m (Fig. 1). We assumed this as the dispersal distance for *R. alpina*, according to empirical data (Drag *et al.* 2011; 80 % of recaptures of marked individuals occurred ≤150 m). The calculation of dPC_k was performed with Conefor Sensinode by applying a probabilistic

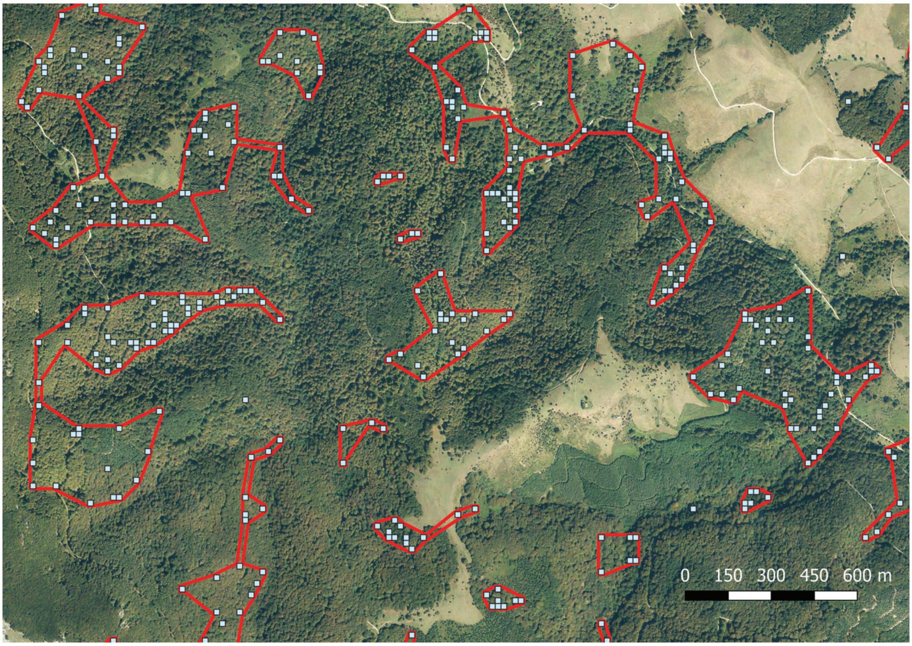


Fig. 1.- Example of selected 20x20-m pixels in a forest massif in Gipuzkoa, indicating potential habitat for *Rosalia alpina* (blue dots), and of patches aggregating pixels less than 150 m apart (polygons in red). These pixels were classified applying a habitat selection model at tree resolution to a LiDAR image (see text for details).

Fig. 1.- Ejemplo de píxeles de 20x20 m seleccionados en un macizo forestal de Gipuzkoa, que indican habitat potencial para *Rosalia alpina* (puntos azules), y de polígonos que enlazan píxeles separados por menos de 150 m (en rojo). Los píxeles se clasificaron aplicando un modelo de selección de habitat a escala de árbol a una imagen LiDAR (ver texto para más detalles).

model of connectivity after a negative exponential function was fitted to the empirical data of maximum likelihood dispersion described by Drag *et al.* (2011):

$$P_{ij} = 0.1613e^{-0.0007 d_{ij}}$$

From a functional point of view, the importance of an element k (node, link) in the landscape was divided into three fractions, after Saura and Pascual-Hortal (2007):

$$dPC_k = dPC\ intra_k + dPC\ flux_k + dPC\ connector_k$$

The fraction dPC_{intra} is the amount of habitat provided by the node itself due to its size (intrapatch connectivity). The fraction dPC_{flux} is defined as the flow through the connections that affect the node when it is the source or destination of that flow. Finally, the fraction $dPC_{connector}$ expresses the contribution of the node to the connectivity among the network of nodes, functioning as a connecting or linking element.

Using the quintiles from the scores obtained for the polygons, these were classified as "core areas" or "connecting areas". In the logical framework of the Landscape Ecology theory, the former are "nodes" and the latter "stepping-stones". The following criteria were applied: (1) core areas were those that, in addition to having a high, medium-high or medium value of the intra fraction of the PC index, also showed medium and medium-high values of the flux fraction; (2) connecting areas were those with high, medium-high and medium values of the connector fraction, or those with medium-low values of the connector fraction and medium or medium-low values of the intra fraction.

Results

We identified 380 polygons (forest patches) of different size, containing structural elements at the tree level required for *R. alpina* (Fig. 2). The largest number of patches and the most important in terms of population connectivity, as ranked by the dPC_k model, were concentrated in south-eastern Gipuzkoa (Fig. 3). This area corresponds

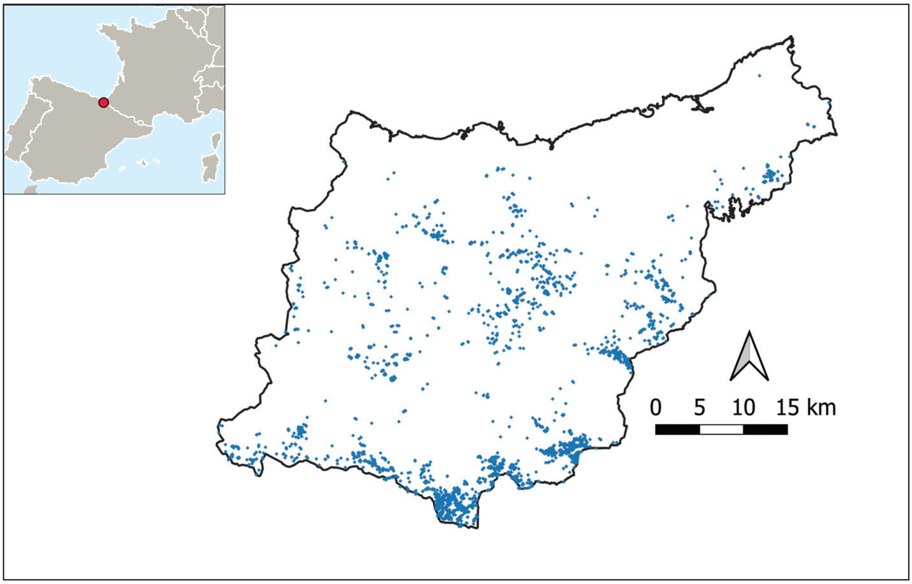
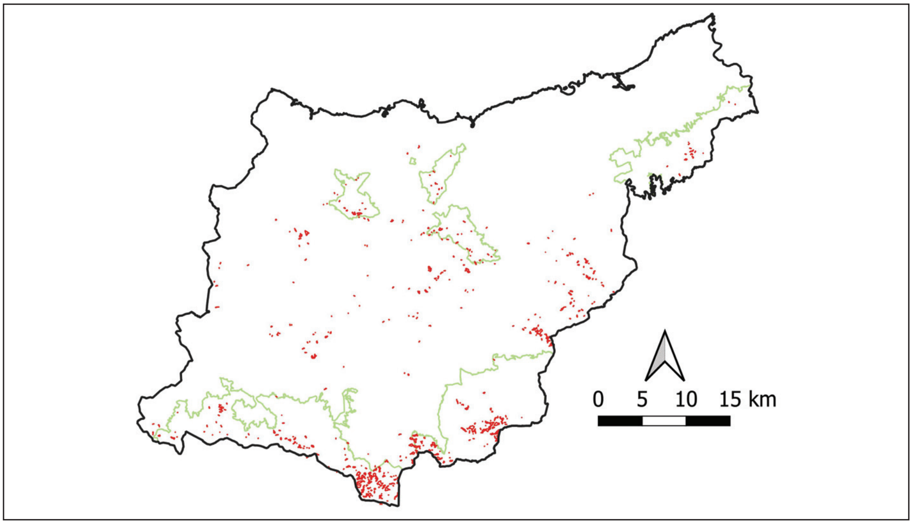


Fig. 2.- Geographical occurrence of 20x20-m pixels indicating potential habitat for *Rosalia alpina* in Gipuzkoa (blue dots). The inset shows the location of the study area in south-western Europe.

Fig. 2.- Rango geográfico de los píxeles de 20x20 m que indican habitat potencial para *Rosalia alpina* en Gipuzkoa (puntos azules). La ubicación del área de estudio en el suroeste de Europa se muestra en el mapa pequeño.



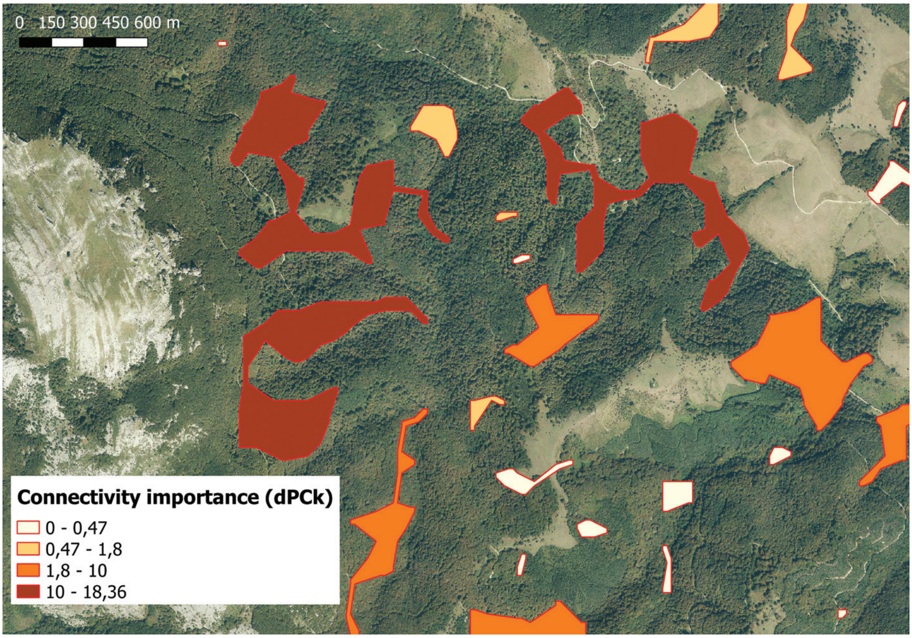


Fig. 3.- Geographical distribution of polygons representing forest patches with structural elements for *Rosalia alpina* in the study area (above; relevant special areas of conservation of the Natura 2000 network are delineated), and example of their importance for the connectivity of the population in a forest massif of Gipuzkoa, based on the dPCk index calculated with Conefor Sensinode software (below).

Fig. 3.- Distribución geográfica de los polígonos que representan parches de hábitat conteniendo elementos estructurales para *Rosalia alpina* en el área de estudio (arriba; se delimitan las zonas especiales de conservación relevantes de la red Natura 2000), y ejemplo de su importancia para la conectividad de la población en un macizo forestal de Gipuzkoa, según el índice dPCk calculado con la aplicación Conefor Sensinode (debajo).

to the mountain ranges of Aizkorri-Aratz and Aralar, which are both classified as Special Areas of Conservation (SAC) within the European Natura 2000 network. No other polygons with such high values were identified in the rest of the study area.

The ratio between ECA and the total surface of the modelled habitat was 19.4, suggesting that the global connectivity for the *R. alpina* population in the study area was low. The largest contribution to the global connectivity of the population was the flux fraction of PC (56.33%); many habitat patches were sources and receptors for dispersing individuals, therefore contributing to metapopulation dynamics at the landscape scale. The intra fraction (37.23%) was less relevant, indicating the existence of fewer patches with sufficient availability of microhabitats to maintain self-sustaining subpopulations. The connector fraction (6.5%) was low, so few patches would be able to act as links in the connectivity system. Only one of the patches in the connecting areas had a high value corresponding to the connector fraction. This suggests deficiencies in the functionality as stepping-stones in most of the patches identified.

Discussion

Model usefulness and limitations

The fragmentation and isolation of the forest patches occupied by saproxylic beetles play a major role in the long-term persistence of populations, precisely because of their limited dispersal abilities (Ranius, 2006; Brunet and Isacsson, 2009; Janson *et al.*, 2009; Brin *et al.*, 2016; Komonen and Müller, 2018), and this impact has been also described for *R. alpina* (Drag *et al.*, 2011). Addressing the connectivity issue by modelling to guide conservation on-ground, especially when complete, systematic data on species occurrence are not readily available, optimises the cost-efficient balance of the action investments for flagship and threatened species (Dudley and Vallauri, 2004; Mizsei *et al.*, 2021), like *R. alpina*. The analysis and proposals in this paper have few precedents regarding saproxylics conservation at the eco-regional level (Nieto and Alexander, 2010).

The previous quantification of the species' ecological niche in the study area (Castro *et al.*, 2012; Castro and Fernández, 2016), the information about relevant aspects of the spatial ecology and demography (dispersal ability, stages and durations of life cycles) of *R. alpina* (Drag *et al.*, 2011) and the availability of remote-sensing data with high resolution allowed us to identify patches of habitat that fit the combinations with high probability of occurrence. This was the only feasible approach to achieve the objective of this study and facilitated the classification of each patch from the point of view of its connectivity function as node or stepping-stone.

The reliability of the ecological niche of *R. alpina* used here (from Castro *et al.*, 2012; Castro and Fernández, 2016) is high, because other studies on habitat preferences published elsewhere in Europe had similar results (Russo *et al.*, 2010; Campanaro *et al.*, 2017). The model by Russo *et al.* (2010) highlighted bark thickness as an influential variable, but in the model for Gipuzkoa bark thickness was assumed to be closely correlated with the availability of forest gaps and insolation. Other independent qualitative approaches to the habitat of *R. alpina* in Gipuzkoa (Pagola, 2011, unpublished report), based on field observations in the Aiako Harria mountain range (NE of the study area), are consistent with the importance of the discontinuities and the sun-exposed clearings inside dense beech forests.

Unfortunately, the identification of deadwood from LiDAR and remote sensing data is not possible yet, less said the characterisation of decay stage, which are fundamental predictors of saproxylic occurrence. But other structural features, like volume, height and DBH are surrogates for presence of tree-related microhabitats (Sebek *et al*., 2013; Kozák *et al*., 2023). Given the forestry history of Gipuzkoa (Aragón, 2010), most existing beech trees that meet the DBH threshold are pollards. These trees have a response profile in the LiDAR image characterised by maximum biomass at 2–3 feet off the ground or a peak more pronounced near the apical zone. The field evaluation endorsed the reliability of our spatially explicit model. LiDAR layers are increasingly used for measuring forest structure across large areas, to encompass species niches reliably (Müller and Brandl, 2009; Zellweger *et al.*, 2014; Davison *et al*., 2023). Moreover, the clustering of selected pixels to generate polygons analysable with Conefor Sensinode improved the modelling performance, because the probability of including favourable microhabitats within these polygons was increased.

Several limitations of the modelling approach have to be acknowledged. Our model did not consider the connectivity with eventual populations at forest patches outside of the study area. Secondly, the connectivity model has only considered the topological (Euclidean distances) relationship among patches, without concerns about the actual permeability of the matrix. However, at the scale of elements interconnected, this matrix consists mainly of regenerating beech forest, so a substantial variability from one relationship to the others is not expected.

R. alpina dispersion and performance of the model

Dispersion of *R. alpina* may be influenced by the species mobility (Komonen and Müller, 2018) and this can be context-dependent (Russo *et al.*, 2010; Drag *et al.*, 2011; Campanaro *et al.*, 2017), but empirical data from the study area was not available. Therefore, there may be concerns about the performance of the scale applied to predict habitat selection and presence of *R. alpina* in Gipuzkoa. However, it has been suggested that low or slightly mobile saproxylics depending on ephemeral resources, like deadwood, use the landscape reaching small patches of habitat in close proximity within larger tracts of unsuitable forest matrix (Winiger *et al*., 2023).

The negative exponential function has been used to describe the distribution of the probability of dispersal related to Euclidean distance in large-bodied saproxylic beetles with low mobility (e. g. *Osmoderma eremita*; Ranius, 2006; Svensson *et al.*, 2011). Empirical dispersal data for *R. alpina* in central Europe were fitted to the function proposed by Drag *et al.* (2011), with an estimation of a median dispersal distance of 161.5 m, close to the 150 m assumed by us to include most dispersal events. It is highly likely that in the forests of Gipuzkoa average movement events are rather short because Castro and Fernández (2016) found in our same study area that 200 m was the maximum distance between the nearest occupied trees by *R. alpina*. Low-frequency, long-distance flights (up to 1.6 km; Drag *et al.*, 2011; Rossi de Gasperis, 2015) may play a role in ensuring gene flow in such spatial configurations. But to delineate potential habitat patches, the average dispersal events are more adequate; therefore, our 150 m threshold seems to adjust to this pattern of ecological use of the landscape. Besides, in our study area, where old-growth habitat patches tend to be clumped within beech forest matrix, dispersal through short-distance flights is probably prevalent.

The identification of core and connecting areas for *R. alpina* in Gipuzkoa were consistent with the expected pattern for a species showing low mobility across fragmented landscapes. Beech forests are concentrated in the south-eastern quadrant of the study area (Dirección General de Desarrollo Rural y Política Forestal, 2013), so the isolation by distance from the remaining beech patches throughout the rest of the territory is extremely high. Moreover, within the larger beech tracts in the South-east, favourable habitat patches with veteran trees are also fragmented, because of the spatial and structural heterogeneity resulting from the history of forest exploitation and the substitution of seminatural forests by plantations. Patches with connector functionality were rarely identified. Overall, the modelling suggested a system in which individuals within each cluster of near habitat patches have little potential difficulty in moving between patches, but dispersal among forest tracts further apart, and the establishment of metapopulation dynamics, proved unlikely.

Conservation implications

Reserve selection and retention techniques through sparing individual trees, groups of trees or small forest patches from exploitation in managed forests have proved particularly beneficial for low o slightly mobile saproxylics (Bouget and Parmain, 2016; Winiger *et al*., 2023). In this context, identification and ranking small forest patches comprising clusters of habitat-trees according to their relevance as nodes and links, can facilitate practitioners the restoration and enhancement of the connectivity for *R. alpina*, because it provides recommendations as to where the interventions will maximize the results.

Although the performance of remote sensing data and complex modelling approaches to aid conservation planning is open to discussion (e.g. Vatka *et al.*, 2014), given the lack of complete and systematic data on distribution, demography, and dispersion of *R. alpina* in the study area, modelling was the logistically most feasible tool to implement scientifically sound conservation (Bosso *et al.*, 2013). For continental or regional-scale management of biodiversity, models have been used successfully to detect core nuclei or gaps in species ranges, recognise or delimitate reserves, corridors, or stepping-stone interconnections (Bosso *et al.*, 2017), as well as to propose sites where restoration actions should be performed (Fitzgerald *et al.*, 2008; Márcia *et al.*, 2010).

Improving the connectivity of the whole population includes modifying some attributes of those patches whose functionality is compromised. This is the most efficient strategy, because it is necessary to increase the ECA over the net increase in habitat surface to achieve improved connectivity. In other words, the restoration of habitat patches in sites lacking possibilities of being colonised would be useless; and restoration in patches that are already connected and part of a metapopulation system would be redundant.

The properties of the landscape must be considered for efficient habitat improvement (Mortelliti, 2013). In our study area, patch size is the most manageable attribute, because the topological position is obviously not an accessible factor, and we lack precise information about the intrinsic structural quality of each patch. According to Brunet and Isacsson (2009) and Sverdrup *et al.* (2010), treatments to improve the availability of microhabitats are more effective if performed at the periphery of selected patches, rather than at locations randomly distributed in the forest landscape, so that the strategy of identifying specific areas for restoration is fully justified.

Management recommendations

The measures most frequently applied to improve the resilience of saproxylic beetle populations include forestry interventions that actively bring stand structure and woodland physiognomy closer to optimal conditions. These conditions are often set on certain types of semi-natural landscapes, like open forests or even pasturelands and parks with big trees in low densities (Jonsell, 2011; Widerberg *et al.*, 2012; Ramírez *et al.*, 2014), along with increasing the volume of dead or decaying wood (Cavalli and Mason, 2003; Davies *et al.*, 2008). Such strategies are based on the theoretical enhancing effect of the increase in the availability of microhabitats provided by veteran and damaged trees, in terms of foraging and breeding resources (Müller *et al.*, 2014).

Based on the relevant scientific literature, management guidelines can be drawn that are applicable to the identified nodes and stepping-stones (Gossner *et al.*, 2013b).

Thus, (1) the optimal patches (nodes) should be strictly preserved to ensure long-term maintenance of the current connectivity, and (2) interventions should be made on those patches that could potentially act as stepping-stones, but whose current conditions only allow poor functionality. For the former, the general approach consists of adopting a protection regime, maintaining clearings, and limiting woodland densification and shrub encroachment.

As for the stepping-stones, silvicultural management should retain in the patch all dead or decaying wood that naturally or artificially occurs. A beech forest patch with less than 20–30 m^3 of dead wood per ha or less than 4–8% of the total volume of timber would not provide sufficient microhabitats for the saproxylic fauna (Dudley and Vallauri, 2004). The average volume of dead wood in the beech forests of Gipuzkoa is 9.0 m^3/ha (Alberdi *et al.*, 2012), far below the one measured in European forest reserves (Christensen *et al.*, 2005). In the periphery of the patch, active interventions should be planned to promote dead or rotting structures (branches, logs, or snags) in the forest canopy and the understory (Cavalli and Mason, 2003; Sebek *et al.*, 2013). To increase sunlight exposure, clearings should be opened, or the density of the patch should be reduced by cutting or uprooting a few trees, either leaving the trunk on the ground or resting it over neighbouring trees (Cavalli and Mason, 2003; Koch *et al.*, 2012).

Concluding remarks

This study presents a feasible approach to identifying high important forest patches for the conservation of *R. alpina*, taking advantage of remote sensing data combined with modelling habitat selection at tree scale. Although these results are only applicable to our own study area, we have shown that connectivity models can inform conservation planning by making reliable predictions and therefore allowing targeted actions. Reserve selection using expert judgement may lead to biased or ineffective options (Saura *et al.*, 2011b). Our emphasis on functional connectivity is justified, because fragmentation of old-growth habitat patches in landscapes dominated by managed, commercial forest stands is a major conservation concern for saproxylic species. Testing in the field the actual performance of the models in terms of real occurrence of *R. alpina*, and the improvements in functional connectivity and conservation prospective for the species achieved with the proposed implementation of regulations and management actions, would be a logical follow-up objective for the future.

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