

# Protecting one, protecting both? Scale-dependent ecological differences in two species using dead trees, the rosalia longicorn beetle and the barbastelle bat

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## Keywords

biodiversity; forest management; Maxent; multiscale analysis; species conservation.

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## Abstract

Organisms sharing the same habitats may differ in small-scale microhabitat requirements or benefit from different management. In this study, set in Italy, we focused on two species of high conservation value, the cerambycid beetle *Rosalia alpina* and the bat *Barbastella barbastellus*, which often share the same forest areas and in several cases the same individual trees. We compared the potential distribution and, at two spatial scales, the niches between such species. The predicted distributions largely overlapped between the beetle and the bat. The niches proved to be similar on a broad scale, yet not on the plot one. Compared with *B. barbastellus*, *R. alpina* tends to occur at lower altitude in more irradiated sites with lower canopy closure and uses shorter trees with wider diameters. *B. barbastellus* occurred more often in trees within forest or along its edges, whereas *R. alpina* lays eggs in trees found in clearings. *B. barbastellus* plots were more frequent in forest, *R. alpina* plots in forested pasture and open-shredded forest. Overall, exposure to sun influenced more critically site and tree selection by *R. alpina*, as a warm microclimate is essential for larval development. Although *B. barbastellus* reproduction may be favored by warmer roosting conditions, bats may also find such conditions in dense forest and in strongly irradiated cavities high up in tall trees that project above the canopy. We emphasize that subtle differences in the ecological requirements of syntopic taxa could be missed at broad scales, so multiple-scale assessment is always advisable.

## Introduction

Species conservation that is undertaken by adopting management practices developed for organisms that apparently share the same habitats and ecological requirements may be tantalizing, yet extremely risky. In fact, syntopic species may often differ markedly in characteristics only revealed at different spatial and/or temporal scales: this may make management practices useful for some species, yet ineffective or even harmful to others (Martin & Lopez, 2002; Russo, Cistrone & Jones, 2005). This is one of the reasons why the so-called 'umbrella species' strategy (managing one species sharing its home range or habitat preferences with several others to benefit a large set of organisms besides the target one) has raised significant concern (Simberloff, 1998; Martin & Lopez, 2002; Roberge & Angelstam, 2004).

Only ecological analyses conducted at multiple spatial scales may reveal spatial or temporal niche differences that

would otherwise go unnoticed, but such studies in conservation biology are still infrequent (Razgour, Hanmer & Jones, 2011). In this study, we test whether a two-scale analysis may reveal differences in two management-dependent forest species that are phylogenetically distant yet apparently share similar habitat preferences: a tree-roosting bat (the barbastelle *Barbastella barbastellus* Schreber) and a saproxylic cerambycid beetle (the rosalia longicorn *Rosalia alpina* L.) whose life cycle largely depends on the availability of dead wood.

*R. alpina* is often mentioned as a flagship species due to its distinctive coloring (Duelli & Wermelinger, 2005; Caci *et al.*, 2013) and is listed as a Priority Species under Annex II of 357/97/EC Habitats Directive. The strong habitat specialization of saproxylic beetles makes them especially vulnerable to human impact (e.g. Berg *et al.*, 1994; Vié, Hilton-Taylor & Stuart, 2009) and exposes them to adverse effects of intensive forestry (Jonsson, Kruys & Ranius, 2005; Jonsson *et al.*,

2006). In summer, adults lay eggs in dead wood, so the species only occurs in patches of mature forest rich with this substrate, as dead wood is necessary for larval development (Duelli & Wermelinger, 2005; Russo *et al.*, 2011a).

*B. barbastellus* is a medium-sized vespertilionid bat featured in Annexes II, IV of the Habitats Directive. Its diet consists largely of moths (Sierro & Arlettaz, 1997), which are hunted in a range of habitats (Hillen *et al.*, 2011; Zeale, Davidson-Watts & Jones, 2012; Ancillotto *et al.*, 2014). Although in some cases *B. barbastellus* maternity groups also roost in live trees (Russo *et al.*, 2010) or even buildings or rock crevices (Ancillotto *et al.*, 2014), typically they are found beneath loose bark on standing dead trees (Russo *et al.*, 2004), where small groups of females gestate, give birth and rear young (Russo *et al.*, 2004).

Despite the very different life cycles, mobility and scales at which saproxylic beetles and snag-roosting bats perceive their habitat and landscapes, both species are threatened by the removal of dead or defective trees. This is one of the typical consequences of commercial forestry in temperate forests (Dudley, Vallauri & France, 2004) driven by concerns over forest health, productivity, fire risk, as well as the spread of pests. Short harvesting rotations characteristic of commercial forestry result in trees being logged before they complete their natural cycle, so that forest turnover will not lead to significant dead wood production (Hunter, 1999). Forestry is a prime cause for the disappearance of reproductive substrate for cerambycids (e.g. Russo, Cistrone & Garonna, 2011a) as well as for the loss of bat roosting habitat (Hayes & Loeb, 2007). Typically, bats roost in small groups spread over large forest areas and switch frequently between roosts (Lewis, 1995), so that the persistence of even a small number of bats requires many trees (Russo *et al.*, 2005). As snags are a rare resource even in unmanaged forests (Russo *et al.*, 2004), the reduction of dead tree density due to forestry has adverse consequences for bats such as *B. barbastellus* that specialize on roosting in snags, especially if they use snags as nurseries (Kurta, Murray & Miller, 2002; Russo *et al.*, 2004).

In the course of previous studies carried out in the Italian Peninsula (Russo *et al.*, 2004; Russo, Cistrone & Jones, 2007; Russo *et al.*, 2010, 2011a), both the bat and the beetle were found to share the same forest areas and in several cases even the same individual trees (Russo *et al.*, 2011a). An apparently obvious assumption would be that as the two organisms may share trees, conservation practices favoring the bat would also benefit the beetle and vice versa. This could be achieved by leaving patches of forest unmanaged and promoting the presence of snags. In our case, two potentially important factors might discourage this approach, (1) the considerable phylogenetic distance between the two species, which may hide subtle yet crucial differences in ecological requirements and (2) the differing mobility and sensitivity to multiple spatial scales linked with their life histories (Russo *et al.*, 2004, 2011a; Drag *et al.*, 2011; Hillen *et al.*, 2011; Ancillotto *et al.*, 2014). For these reasons, variables other than tree type might influence selection patterns in different ways and only reveal themselves at specific spatial scales.

Our study was based in Italy, where both species occur sympatrically and sufficient data were available for our modeling exercise. We carried out a comparison between *R. alpina* and *B. barbastellus* and hypothesized that differences in ecological requirements, if any, could emerge at a small spatial scale (i.e. the tree used and its immediate surroundings), best reflecting microhabitat needs. If the ecological needs of the two species differ, conserving the bat and the beetle would require a multiple spatial scale approach within areas of sympatry and *ad hoc* management practices. Although previous studies had analyzed tree and habitat selection in *B. barbastellus* (Russo *et al.*, 2004) and *R. alpina* (Russo *et al.*, 2011a) and developed a spatially explicit model for the latter (Bosso *et al.*, 2013) to offer a basis for gap analysis, ours is the first that compares the two species' ecological requirements at two markedly different spatial scales to explicitly test whether common management strategies may be revealed at either scale and adopted to improve the status of two taxa of conservation concern.

Within this framework, we generated the following predictions:

- (1) The co-occurrence of the two species in areas characterized by old-growth stands will lead to significant overlap in their potential distribution and similarity in ecological needs estimated using factors selected at a broad geographical scale.
- (2) At a smaller scale, *R. alpina* will prefer trees in semi-open habitat whose immediate surroundings favor sun irradiation, a factor deemed of vital importance for the development of larvae (Russo *et al.*, 2011a; Duelli & Wermelinger, 2005; Bosso *et al.*, 2013). On the other hand, although reproductive females of *B. barbastellus* may be favored by roosting in sun-exposed cavities, they may do so in dense forest too by roosting higher up in trees (Russo *et al.*, 2004, 2007). Roosting in more forested habitats would shelter emerging bats from aerial predators and allow them to start foraging earlier (Russo *et al.*, 2007). Therefore, unlike *R. alpina*, the bat will tend to occur in more densely forested habitats and will select taller trees.

## Materials and methods

### Study area

We considered the entire Italian territory between latitudes 45°N–36°N and longitudes 6°E–18°E (corresponding to c. 301,000 km<sup>2</sup>, elevation range = 0–4810 m a.s.l.) including the Alpine, Continental and Mediterranean biogeographical regions according to the EC/92/43 Habitats Directive classification.

### Model development and validation

Presence records for *R. alpina* ( $n = 350$ ) and *B. barbastellus* ( $n = 223$ ) originated from the authors' personal databases and previous publications (Russo *et al.*, 2004, 2005, 2010; Bosso *et al.*, 2013). Records were screened in ArcGis version 9.2 (Environmental Systems Research Institute Inc., Redlands, CA, USA) using average nearest neighbor analyses and



**Figure 1** Presence records of *Rosalia alpina* (black dots) and *Barbastella barbastellus* (grey dots) considered for the development of a maximum entropy model.

Moran's I measure of spatial autocorrelation to remove spatially correlated data points and guarantee independence and equivalence to random sampling. After this selection, 37 and 25 data, respectively, for *R. alpina* and *B. barbastellus* were used to generate species distribution models and niche analysis (Fig. 1).

All *B. barbastellus* data used to generate the models were collected between 2000 and 2013, while 82% of *R. alpina* records were collected between 2000 and 2010 and the remaining 18% between 1990 and 2000. Overall, this ensured a good temporal matching with the time period of the land cover map production (2006).

In the recent ecological literature, a diversity of meanings is attributed to the term 'niche' so that to avoid confusion constant qualification is advisable (McInerney & Etienne, 2012). In this paper, we follow Phillips, Anderson & Schapire (2006) and assume that environmental conditions at the occurrence localities represent samples from the realized niche. Therefore, given a certain study area and the corresponding environmental dimensions, a niche-based model provides an approximation of the species' realized niche.

To generate models and carry out niche analysis for *R. alpina* and *B. barbastellus*, we used a set of 21 environmental predictor variables. We included one topographical and 19 bioclimatic variables obtained from the WorldClim database ([www.worldclim.org/current](http://www.worldclim.org/current)) (Hijmans *et al.*, 2005). Land

**Table 1** List of ecogeographical variables used for this study, type and measurement unit

Type	Ecogeographical variable	Unit
Topographical	Altitude	m
Habitat	Land cover	–
Climatic	Mean diurnal range	°C
	Isothermality	%
	Temperature seasonality	°C
	Temperature annual range	°C
	Mean temperature of wettest quarter	°C
	Mean temperature of driest quarter	°C
	Precipitation seasonality	%
	Precipitation of wettest quarter	mm
	Precipitation of coldest quarter	mm

cover was obtained from Global Land Cover 2000 (<http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais/corine-land-cover>). All variable formats were raster files (grid) with a resolution of 30 arc seconds ( $0.93 \times 0.93 \text{ km} = 0.86 \text{ km}^2$  at the equator) and 1 307 195 grid cells. In order to remove the highly correlated variables for the final distribution models, we calculated a correlation matrix using the Pearson's correlation coefficient and selected only variables which showed a weak correlation with the others ( $r < 0.5$ ), as performed in Russo *et al.* (2014). We came up with 11 final environmental predictor variables and used them to model habitat suitability and niche analysis of both species in ASCII files. Bosso *et al.* (2013) also developed a species distribution model for *R. alpina*, but in the present study we generated a new model as niche comparison required use of the same environmental predictor variables for both species.

We used the most applied method with scarce presence-only data to develop species distribution models for *R. alpina* and *B. barbastellus*, that is Maxent ver. 3.3.3k (<http://www.cs.princeton.edu/~schapire/maxent>). This method usually results in good predictive models compared with other presence-only models (e.g. Elith *et al.*, 2006). It uses a generative approach, rather than a discriminative one, which can be an important advantage when the amount of training data is limited (Phillips *et al.*, 2006). Furthermore, it has a good ability to predict new localities for poorly known species (Rebello & Jones, 2010; Bosso *et al.*, 2013; Russo *et al.*, 2014).

To build the models, we used the presence records for *R. alpina* and *B. barbastellus* selected as described earlier and the following environmental predictor variables: altitude, land cover, mean diurnal range, isothermality, temperature seasonality, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, precipitation seasonality, precipitation of wettest quarter and precipitation of coldest quarter. Further details on environmental predictor variables are given in Table 1.

Although altitude is an indirect variable usually correlated with other direct variables such as temperature, we used it because it was easily recorded for the plot-level analysis and applied to the two-scale analyses for consistency.

In the setting panel, we selected the following options: random seed, remove duplicate presence records, write plot

data, regularization multiplier (fixed at 1), 10 000 maximum number of background points, 1000 maximum iterations and, finally, 20 replicate effects with cross-validate replicated run type. For the latter procedure, 80% of records were randomly extracted for training and 20% for testing the model and the procedure was repeated 20 times. The average final map obtained had a logistic output format with suitability values from 0 (unsuitable habitat) to 1 (suitable habitat).

We used Jackknife analysis to estimate the actual contribution that each variable provided to the geographic distribution models. During this process, Maxent generated three models: first, each environmental predictor variable was excluded in turn and a model was created with the remaining variables to check which of the latter was most informative. Second, a model was created using each environmental predictor variable individually to detect which of them had the most information not featured in the others. Third, a final model was generated based on all variables. Response curves derived from univariate models were plotted to determine how each environmental predictor variable influences the probability of presence.

For the placement of pseudo-absence points following Barve *et al.* (2011) as background area, we used all ecoregions found in the Italian Peninsula including presence points.

We tested the predictive performance of the models with different methods: the receiver operated characteristics, analyzing the area under curve (AUC) (Fielding & Bell, 1997); the true skill statistic (TSS) (Allouche, Tsoar & Kadmon, 2006); and the minimum difference between training and testing AUC data (AUC<sub>diff</sub>) (Warren & Seifert, 2011). Such statistics were averaged across the 20 replicates run on the 80% (training) versus 20% (testing) dataset split. These model evaluation statistics range between 0 and 1: excellent model performances are expressed respectively by AUC and TSS values close to 1 and AUC<sub>diff</sub> close to 0.

### Protecting one, protecting both? Scale-dependent niche differences

We performed niche overlap analyses using the analytical framework proposed by Broennimann *et al.* (2012) and recently adopted by Di Febbraro *et al.* (2013) and Russo *et al.* (2014). The procedure follows three steps: data pre-processing, calculation of the niche overlap measure and testing niche similarity. For niche comparison, we used the Schoener's D index, ranging from 0 (no overlap) to 1 (niches identical). This index was calculated using the 'ecospat' package ([ran.r-project.org/web/packages/ecospat/index.html](http://ran.r-project.org/web/packages/ecospat/index.html)). Further details are given in Di Febbraro *et al.* (2013).

Niche analysis was conducted both at broad and plot scales. At a broad scale, corresponding to the whole Italian territory, we compared the differences in environmental predictor variable values used to build the species distribution models between species. To quantify niche overlap, we used the ordination method of principal component analysis calibrated on the whole environmental space including the presence records where the species occur (for details see Broennimann *et al.*, 2012).

We also compared the niches of *R. alpina* and *B. barbastellus* at the plot scale by exploring differences in tree and site descriptors for 42 trees used by the former for reproduction and 66 nursery roosts of the latter occurring in the same study area (Abruzzo, Lazio and Molise National Park). Our plots are represented by the focal tree and the characteristics found in the space corresponding to its canopy. Trees were found in earlier studies (Russo *et al.*, 2004, 2005, 2007, 2010, 2011a) in which adults of *R. alpina* were observed inspecting suitable trees and *B. barbastellus* roosts were found by capturing bats at drinking sites, fitting them with radiotags and tracking them in daytime to their roost trees (see Russo *et al.*, 2004, 2011a for further details on methodology). Following Russo *et al.* (2011a) we considered the following features: (1) tree diameter at breast height (in meter); (2) tree height (in meter, obtained with a clinometer); (3) percentage of canopy closure (assessed visually as the percentage of the tree's branches and foliage which was in contact with those of surrounding trees); (4) sun index (estimated on a 0–12 scale: 0, fully shaded tree; 12, sun from all directions); (5) tree condition (live; dead and fallen tree); (6) crown condition (full foliage, foliage or branches partly missing, crown absent); (7) tree position (in forest, in clearing, on forest edge); (8) undergrowth height (0, between 0 and 1 m and > 1 m); (9) altitude (in m a.s.l.); and (10) habitat type (forest, forested pasture and open-shredded forest). 'Forest' corresponded to stands mainly unlogged since 1956 or subject to occasional very limited and highly selective logging; 'forested pasture' was characterized by pastures interspersed with (or surrounded by) old trees present at low densities and shrubs; and 'open-shredded forest', so called because trees used to be pruned by 'shredding' (removing all side branches), a traditional form of management aimed to keep open space for pasture and use removed branches and foliage as animal fodder (Russo *et al.*, 2011a).

To quantify niche overlap at plot scale, we used the factor analysis for mixed data (FAMD) calibrated on the aforementioned records. FAMD is a principal component method to explore datasets including both continuous and categorical variables. The continuous variables are scaled to unit variance and the categorical variables are transformed into a disjunctive data table (crisp coding) in order to balance the influence of both continuous and categorical variables in the analysis.

To explain niche differences between species at both scales, we compared environmental predictor variables recorded at presence points and plot descriptors measured in the field on trees used with an analysis of variance followed by a Tukey's *post hoc* test and  $\chi^2$ -test at *P*-value < 0.05 using XLSTAT version 2013.1 (Addinsoft, Paris, France).

## Results

### Broad geographical scale – model development and validation

As predicted, at the broad geographical scale, the potential distribution generated by our models for the two species largely overlapped. The model for *R. alpina* identified sub-





**Figure 2** Maximum entropy model developed for *Rosalia alpina* (left) and *Barbastella barbastellus* (right) in Italy. Likelihood of species occurrence is expressed as shades of grey (white = 0, black = 1).

**Table 2** Predictive performances achieved for species distribution models developed for *Rosalia alpina* and *Barbastella barbastellus*

Species	AUC training	SD	AUC test	SD	AUC <sub>diff</sub>	SD	TSS	SD
<i>Barbastella barbastellus</i>	0.953	0.004	0.918	0.029	0.035	0.003	0.701	0.112
<i>Rosalia alpina</i>	0.948	0.011	0.914	0.014	0.034	0.002	0.721	0.155

AUC, area under curve; AUC<sub>diff</sub>, difference between training and testing AUC data; SD, standard deviation, TSS, true skill statistic.

stantially uninterrupted areas of occurrence in Italy from the Alps to southern Apennines (Fig. 2). In the remaining area, only a few scattered sites were predicted as suitable. The model for *B. barbastellus* predicted a high probability of presence in the central Apennines, as well as in the southern Apennines and in the western Alps.

The environmental predictor variable sets contributing the most to the models for the two species were similar. In the *R. alpina* model (limiting our analysis to environmental predictor variables with percentage of contribution > 2%), land cover (45%) and altitude (36%) were the main factors influencing model performance. A slightly lower contribution was provided by isothermality (9%), precipitation seasonality (5%), mean temperature of driest quarter (2.4%) and precipitation of coldest quarter (2.4%). Based on the model's predictions, *R. alpina* has a higher probability of occurring in broadleaved deciduous forest found at relatively high altitudes (1000–1500 m a.s.l.). The environmental predictor variables that were most important to explain the potential distribution

of *B. barbastellus* were: land cover (47%), altitude (27%), mean temperature of driest quarter (10%), isothermality (8%), precipitation seasonality (4%) and precipitation of coldest quarter (2.1%). We observed that in the areas predicted as suitable for *B. barbastellus* (Fig. 2), land cover was mainly characterized by broadleaved deciduous forest and deciduous shrubs. Furthermore, in those areas altitude ranged between 1000 and 1500 m a.s.l. and the mean temperature of the driest quarter between 15 and 20°C.

Species distribution models achieved excellent levels of predictive performance for *R. alpina* and *B. barbastellus* as seen from the AUC, TSS and AUC<sub>diff</sub> values (Table 2).

### Protecting one, protecting both? Scale-dependent niche differences

The outcome of niche similarity tests greatly depended on the scale considered. In agreement with our first prediction, the two species' niches were similar at a broad geographical scale,

**Table 3** Outcomes of niche equivalence and niche similarity tests for *Rosalia alpina* and *Barbastella barbastellus* at broad (Italy) and plot (tree and its immediate surroundings) scales

Scale	Method	Schoener's D	Niche equivalency	Niche similarity	
				<i>R. alpina</i> → <i>B. barbastellus</i>	<i>B. barbastellus</i> → <i>R. alpina</i>
Broad	PCA-ENV	0.487	0.01	0.01	0.01
Plot	FAMD	0.319	0.003	NS	NS

FAMD, factor analysis for mixed data; NS, not significant; PCA-ENV, principal component analysis calibrated on the whole environmental space including the presence records where the species occur.

yet they were rather different at the plot scale (Table 3). The graphical representation of the niches of the two species in environmental space at both scales is shown in Fig. 3.

At a broad spatial scale, relatively few differences were spotted between the potential areas of occurrence for the two species, their large-scale ecological requirements being mostly similar (Fig. 3; Table 4). *B. barbastellus* was found to occur in areas whose mean temperature of driest quarter, precipitation seasonality, and to some extent isothermality, were significantly greater than those of areas occupied by *R. alpina* (Fig. 3). Although both species mostly occurred in similar land use types, *B. barbastellus* was predicted to occur in cultivated and managed areas more often than *R. alpina*, whereas the latter was more often predicted to occur in mosaics of tree cover interspersed with other natural vegetation and in semi-open areas of shrubland and deciduous forest.

At a plot scale, in accordance with our second prediction, we identified marked differences in the type of habitat used by the two species (Fig. 3; Table 4). Although both species may occur in the same plot and share the same tree, *R. alpina* tends to occur at sites characterized by a lower altitude, lower canopy closure, higher sun index (i.e. sites are more irradiated) and to select (live or dead) shorter trees with a larger diameter than *B. barbastellus* (Figs 3 and 4). The trees used by *B. barbastellus* (mostly snags) occurred significantly more often within forests or along forest edges, whereas *R. alpina* tends to lay eggs in trees found in clearings.

*B. barbastellus* plots were significantly more frequent in forest, while those of *R. alpina* were more frequent in forested pasture and open-shredded forest (Table 4).

## Discussion

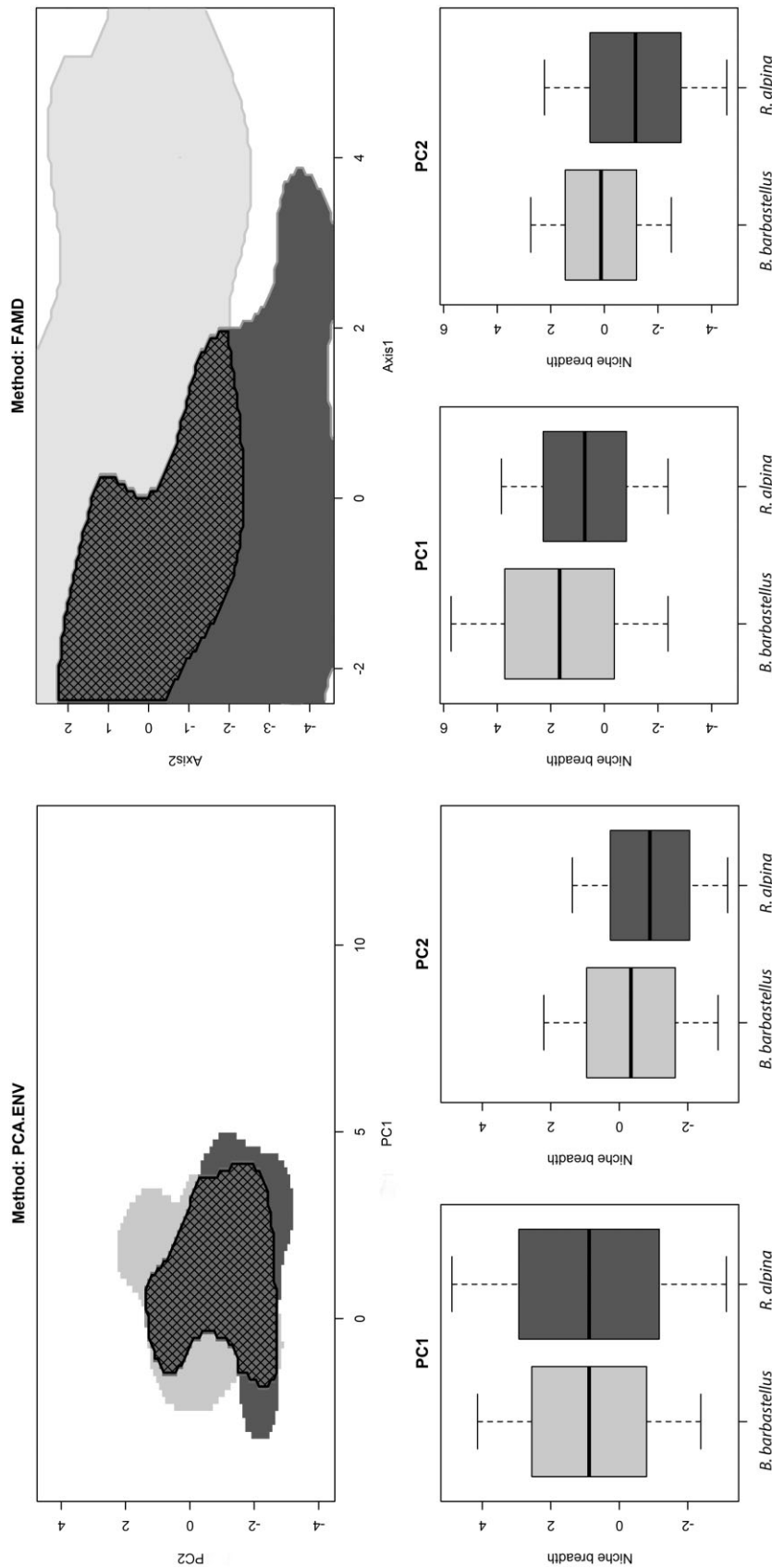
### Scale-dependent niche differences between *R. alpina* and *B. barbastellus*

Our study showed that two organisms largely dependent on dead wood for a crucial part of their life cycle (reproduction), despite being found in the same areas and sometimes in the same tree, exhibit different ecological requirements that mostly emerge when niches are compared at a small spatial scale. A broad geographical scale is too coarse-grained to reveal considerable differences. In accordance to our first hypothesis, the broad scale analysis essentially shows that the two species are largely sympatric and syntopic, occurring in the same areas of broadleaved forest, while failing to detect differences in microhabitats occupied.

At a large scale, only limited differences in preferred environmental predictor variables values were detected. Besides a small difference in isothermality (= mean diurnal range/temperature annual range, expressing temperature 'evenness' over a year), *B. barbastellus* tends to occur in areas characterized by a higher temperature of the driest quarter than does *R. alpina*. Such mild conditions in the season when bats are active are important for reproduction. Pregnancy and lactation are energy-demanding because during these phases females need to be homeothermic and avoid using torpor to allow fetal development and to provide milk for their young (Racey, 1973; Grinevitch, Holroyd & Barclay, 1995). Higher roost temperatures (inevitably influenced by ambient temperature) reduce thermoregulatory costs and may thus be favorable for females during pregnancy and lactation (Grinevitch *et al.*, 1995). Higher nocturnal temperatures also increase insect activity (Taylor, 1963) and thus bat foraging (Russo & Jones, 2003). For *R. alpina*, spring temperatures are more important than summer temperatures (Bosso *et al.*, 2013): at least some warmth is needed daily in spring for larval development, when larvae build pupal cells beneath bark where they will eventually undergo metamorphosis in summer (Duelli & Wermelinger, 2005).

We found the potential distribution of the two species to largely overlap in terms of land use types, with both species predicted to occur in areas dominated by broad-leaved forest. *B. barbastellus* was also predicted to occur in cultivated and managed areas more often than *R. alpina*. The beetle was instead predicted to occur more in mosaics of tree cover interspersed with other natural vegetation and in semi-open areas of shrubland and deciduous forest. *B. barbastellus* forages in a broad range of habitats (Hillen *et al.*, 2011; Zeale *et al.*, 2012), including farmland, which may locally be of great importance (Ancillotto *et al.*, 2014). In contrast, the more marked preference for semi-open landscapes detected for *R. alpina* may reflect its tendency to lay eggs in well-exposed trees (Duelli & Wermelinger, 2005; Russo *et al.*, 2011a; Bosso *et al.*, 2013) – which, as we will see, was revealed by plot-level comparisons.

Apart from these limited differences, the overlap of the species' potential distributions suggests that wide areas of syntopy can be protected, providing conservation benefits to both the beetle and the bat. In Italy, over 52% of habitat suitable for *R. alpina* is unprotected (Bosso *et al.*, 2013). Given the distributional overlap, we may assume that the potential distribution of *B. barbastellus* also largely falls out of boundaries of parks and reserves. Broad scale analysis,



**Figure 3** Graphical representation of the environmental niches of *Rosalia alpina* (dark grey) and *Barbastella barbastellus* (light grey). The upper left panel represents the niche of the two species along the two-first axis (PC1 and PC2) of the principal component analysis (PCA-ENV) calculated at broad scale. Increasing values of PC1 mainly correspond to increasing precipitation of coldest quarter and decreasing mean diurnal range [mean of monthly (maximum temperature – minimum temperature) and mean temperature of wettest quarter. Increasing values of PC2 mainly correspond to increasing values of isothermality, mean temperature of driest quarter and precipitation seasonality (coefficient of variation)]. The upper right panel shows the species' niches along the two-first axis (Axis1 and Axis2) of the factor analysis for mixed data (FAMD) calculated at plot scale. Increasing values of PC1 mainly correspond to increasing percentage of canopy closure and tree height and decreasing sun index and tree diameter, whereas PC2 mainly increases with altitude and tree height. For each scale, the corresponding box-and-whisker plots illustrated below represent the median, quartiles, and extremes of the two component values.

**Table 4** Statistical comparisons (analysis of variance or chi-square test) respectively of environmental predictor variables values used to build the species distribution models on a broad geographical scale (Italy) and of plot characteristics measured in an area of sympatry (in central Italy) between *Rosalia alpina* and *Barbastella barbastellus*

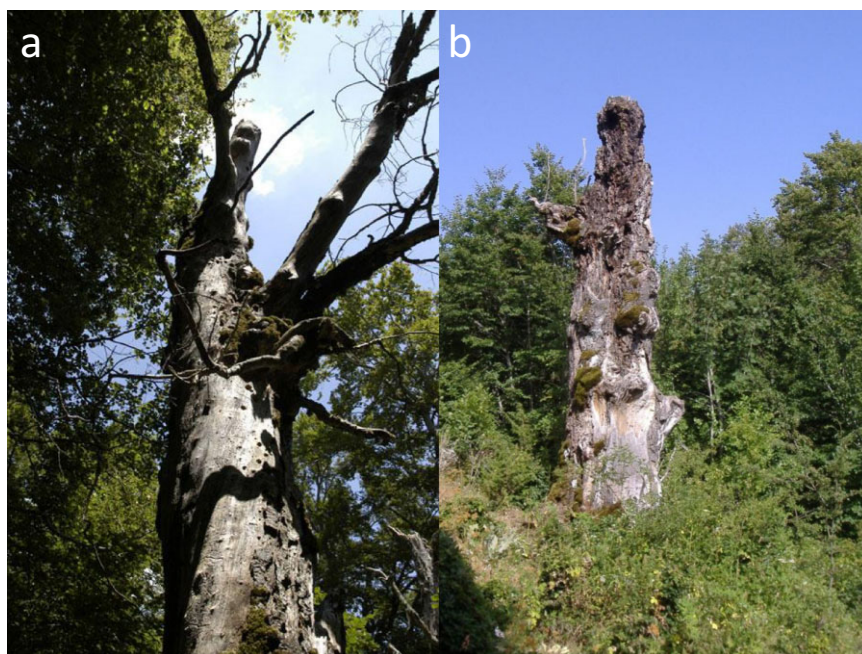
Italian territory				
Variable	<i>B. barbastellus</i>	<i>R. alpina</i>	Statistics	<i>P</i>
Altitude (m)	984.91 ± 401.08	1100 ± 377.21	1.51 <sup>a</sup>	NS
Annual mean diurnal range (°C)	7.64 ± 1.03	7.11 ± 1.43	3.04 <sup>a</sup>	NS
Annual temperature range (°C)	25.01 ± 1.82	24.58 ± 2.32	0.87 <sup>a</sup>	NS
Isothermality (%)	29.97 ± 2.24	28.25 ± 3.45	5.91 <sup>a</sup>	0.01
Land cover			25.65 <sup>b</sup>	0.04
Mean temperature of driest quarter (°C)	16.45 ± 6.46	11.98 ± 8.70	5.75 <sup>a</sup>	0.01
Mean temperature of wettest quarter (°C)	8.83 ± 3.1	9.06 ± 3.22	0.09 <sup>a</sup>	NS
Precipitation of coldest quarter (mm)	213.02 ± 33.47	207.37 ± 35.29	0.46 <sup>a</sup>	NS
Precipitation of wettest quarter (mm)	283.88 ± 37.80	293.80 ± 48.43	0.89 <sup>a</sup>	NS
Precipitation seasonality (%)	28.67 ± 9.57	27.51 ± 7.11	0.32 <sup>a</sup>	NS
Temperature seasonality (%)	6125.23 ± 303.46	6146.85 ± 369.86	0.02 <sup>a</sup>	NS
Plot scale				
Altitude	1487.26 ± 115.78	1384.45 ± 137.54	7.86 <sup>a</sup>	0.01
Undergrowth height			0.36 <sup>b</sup>	NS
Canopy closure	32.76 ± 37.71	13.80 ± 29.40	7.54 <sup>a</sup>	0.01
Crown condition			0.48 <sup>b</sup>	NS
Habitat type			22.81 <sup>b</sup>	0.01
Tree condition			21.89 <sup>b</sup>	0.02
Sun index	5.01 ± 3.32	9.85 ± 2.90	5.70 <sup>a</sup>	0.01
Tree diameter	0.92 ± 0.24	1.03 ± 0.31	4.14 <sup>a</sup>	0.03
Tree height	20.36 ± 7.66	8.05 ± 4.81	8.55 <sup>a</sup>	0.01
Tree position			34.80 <sup>b</sup>	0.01

Sample size for Italy: *n* = 25 (*B. barbastellus*), *n* = 37 (*R. alpina*), broad scale; *n* = 66 (*B. barbastellus*), *n* = 42 (*R. alpina*), plot scale.

<sup>a</sup>F.

<sup>b</sup>χ<sup>2</sup>.

NS, not significant.

**Figure 4** Typical trees selected by *Barbastella barbastellus* (a) and *Rosalia alpina* (b) in central Italy.



however, reveals little of the detailed ecological differences characterizing the two species and gives no information on the type of management that the two species need.

In agreement with our second prediction, the niche comparison conducted at plot scale revealed marked differences in the ecological requirements of the two organisms, clearly rejecting the hypothesis that simply preserving snags in areas of syntopy will necessarily favor both taxa. The first obvious difference is that trees frequented by *R. alpina* had a much smaller canopy closure (on average almost one-third of that recorded for *B. barbastellus* roosts). Consequently, these trunks are much more exposed to sun than those used by the bat, as can be seen by their significantly greater sun index. Such trees were also found to occur more often in clearings than those used by *B. barbastellus*, which were more frequent in forest interiors. Exposure of reproductive substrate to the sun is of utmost importance for many saproxylic beetles, as it provides the microenvironmental conditions that larvae require to develop (e.g. Lindhe, Lindelöw & Åsenblad, 2005; Buse, Schröder & Assmann, 2007; Vodka, Konvicka & Cizek, 2009).

In the study area we focused on, clearings resulted from traditional shredding to open space for livestock grazing (Russo *et al.*, 2011a). Shredded trees often attain large diameters and smaller heights, explaining the structural differences we found between trees favored by *R. alpina* and *B. barbastellus*. For *B. barbastellus*, tall trees are important as bats tend to roost close to the canopy (Russo *et al.*, 2004). Roosting at height is important for at least two reasons: first, bats are less accessible to predators; second, snag tops often protrude out of the canopy, allowing roosts to be irradiated even in dense forest (Russo *et al.*, 2004, 2007). By selecting such roosts, reproductive females may achieve lower-cost thermoregulation while gaining some extra foraging time through earlier roost emergence in a cluttered habitat, where predation risks are lower (Russo *et al.*, 2007, 2011b). Female *B. barbastellus* roosting in dead trees may be favored by the absence of living wood tissue, which reduces temperatures in roost trees (Law & Anderson, 2000). Along with the presence of loose bark providing roosting spaces, this is probably why the bat occurred more often in snags than did the beetle, also found in live trees that included some dead parts where eggs are laid.

*B. barbastellus* plots were more frequent within the forest (which is mostly unmanaged or subject to very little management in the study area), whereas *R. alpina* plots occurred more often within open-shredded forest and forested pasture. This result is in agreement with habitat selection studies carried out in the same area (Russo *et al.*, 2005, 2011a) and matches well with tree structural characteristics preferred by the two species.

Despite the co-occurrence of *R. alpina* and *B. barbastellus* often in the same habitats and sometimes even in the same trees, the plot-level analysis revealed important differences in both habitat type and tree descriptors, indicating that different types of management may be required for the two species. This once more highlights that avoiding confusion between 'used' and 'preferred' resources or conditions is crucial and emphasizes the need to support management with sound scientific data instead of relying on merely qualitative observation-driven 'expert judgment' which may be misleading.

Clearly, practices such as girdling may favor both *R. alpina* and *B. barbastellus* (Russo *et al.*, 2010, 2011a) by increasing snag density but will not suffice to grant these species the conditions they require. In conclusion, fully reconciling the management requirements of the two species appears to be unviable on a tree/habitat scale: while the beetle would benefit from clearing some surrounding trees, the bat prefers its roosts to be protected by a denser canopy closure. Leaving unmanaged forest patches will increase the availability of dead wood (e.g. Ranius & Jansson, 2000), yet it will also lead to the expansion of closed forest avoided by *R. alpina*, at the expense of the beetle's preferred habitat.

In areas of syntopy, successful management may only be achieved through a landscape approach, that is by allowing the interspersed forest patches with clearings and semi-open areas where trees are more exposed to the sun. In the Italian Apennines, this landscape mosaic was once typical of traditionally exploited forest, when humans were more widespread in the mountains, and is now disappearing along with the loss of non-intensive management such as shredding and moderate livestock grazing. Today, grazing intensity is in fact polarized, some areas being subjected to unsustainable livestock loads and consequently overgrazed, while others that were formerly semi-open are being invaded with regrowth of vegetation due to the absence of grazing by herbivores (Moreira & Russo, 2007).

## Conservation implications

Our study has clear implications for conservation and management. First, it shows that important ecological differences may be unveiled only at one scale of analysis and missed at others (Levin, 1992). Predicting distribution ranges by modeling may offer important guidance in the development of conservation plans, for example by allowing more exhaustive gap analyses than when conducted only on ranges established on presence data (Bosso *et al.*, 2013); by helping detect corridors or low-suitability areas in need of restoration to improve connectivity (Doko *et al.*, 2011); by making it possible to predict future distribution patterns under climate or land use change (Rebelo & Jones, 2010; Rebelo, Tarroso & Jones, 2010); or by assisting in the discovery of new areas of occurrence for rare species (Rebelo & Jones, 2010). However, subtle differences in ecological requirements could be missed at broad analysis scales, so it is always advisable to carry out analyses at multiple scales. We also once more highlight the value of a landscape approach to compromise the ecological requirements of species of conservation concern that may appear conflictual at habitat scale and emphasize the importance of heterogeneity typical of traditional landscapes, shaped by hundreds of human generations (Di Salvo *et al.*, 2009; Georgiakakis *et al.*, 2010), to sustain diversity-rich communities.

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