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ORIGINAL ARTICLE

Microhabitat use and co-occurrence patterns of *Rosalia alpina* and *Morimus asper funereus* (Coleoptera: Cerambycidae) in an old-growth beech forest, Triglav National Park, Slovenia

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Abstract. Saproxylic beetles are among the most important forest invertebrates associated with dead and decaying wood, yet many species are threatened by the loss of old-growth forest structures. We investigated the microhabitat use, demography and dispersal of two saproxylic longhorn beetles, *Rosalia alpina* (Linnaeus 1758) and *Morimus asper funereus* Mulsant 1863, in a system of 12 habitat patches within a forest reserve in Triglav National Park, Slovenia. We examined 30 potentially suitable trees and marked 68 individuals of *M. a. funereus* and 37 individuals of *R. alpina*. Generalised linear mixed models showed contrasting habitat preferences between the two species. *M. a. funereus* strongly preferred standing, dying beech (*Fagus sylvatica*) trees with large diameters, whereas *R. alpina* showed no significant preference for any studied tree category and displayed a patchy distribution. These patterns suggest ecological niche differentiation and possible resource partitioning between the species. The best-fit POPAN open population model (φ_{tlin} p_{tlin} $b_{tlin+tlin^2}$) estimated the population size of *M. a. funereus* at 144 individuals (95% confidence interval 88–199), with high but gradually declining survival and peak recruitment in early August. For *R. alpina*, a population size estimate was not possible due to sparse recaptures; however, an extensive area of contiguous beech forest near the study area extends the suitable habitat for both species. *M. a. funereus* made predominantly short-distance movements (maximum 34 m), whereas *R. alpina* undertook less frequent but substantially longer movements (maximum 457 m), indicating greater dispersal ability. Our results highlight the importance of structurally diverse old beech forests with abundant dead and dying trees for the persistence of both species and suggest that differences in habitat use and mobility may reduce direct competition in sympatry.

INTRODUCTION

Old, dying, and dead trees represent key structural elements of mature forest ecosystems, providing essential habitats for a wide range of organisms, particularly saproxylic species (Dudley & Vallauri, 2004). Their availability has declined markedly in European forests due to intensive management practices such as logging and deadwood removal (Dudley & Vallauri, 2004; Müller et al., 2008). In temperate forests, large old-growth beech trees (*Fagus sylvatica*) are especially important, supporting diverse assemblages of saproxylic insects and fungi (Jurc, 2004, 2012). Saproxylic insects depend on dead or dying wood for part of their life cycle, using it for larval development, shelter, or reproduction (Speight, 1989; Stokland et al., 2012). Many species are specialised to particular decay stages, tree sizes, or microhabitat conditions such as sun exposure and tree position (standing vs. fallen), making them sensitive to changes in forest structure and management. Large-diameter trees are particularly valuable, as they provide more stable microclimatic conditions, higher wood volume, and longer-lasting resources (Jurc, 2004; Ranius, 2002).

Among saproxylic beetles, longhorn beetles (Cerambycidae) include several flagship species with high conservation relevance. Two of these are the Alpine longhorn beetle *Rosalia alpina* (Linnaeus, 1758) and the beech longhorn beetle *Morimus asper funereus* (Mulsant, 1863). *R. alpina* is a priority species listed in Annex II of the EU Habitats Directive (Council of Europe, 1992) and included in the IUCN European Red List of saproxylic beetles (Cálix et al., 2018), with populations declining across much of its range due to habitat loss and fragmentation. It primarily develops in sun-exposed dead or dying beech trees, and adults are capable flyers frequently observed on large trunks during summer (Drag et al., 2011; Russo et al., 2011). *M. a. funereus* is closely associated with large, decaying beech

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trees and, while not listed in Annex II, is of high conservation concern in Europe (Solano et al., 2013; Danilevsky, 2022). Despite overlapping associations with large beech trees and decaying wood, ecological data on these two species remain incomplete and are often restricted to single biogeographical regions (e.g. *R. alpina*: habitat preferences – Russo et al., 2011; Fernández-García et al., 2023; demography and movements – Drag et al., 2011; *M. asper/funereus*: overview of ecology and ethology – Hardersen et al., 2017; habitat suitability – Kostova et al., 2023). In particular, little is known about their fine-scale microhabitat preferences when occurring sympatrically, or about potential interspecific interactions arising from shared use of limited woody resources. Such interactions may be especially relevant in managed forests, where suitable large-diameter trees are scarce and spatially aggregated.

In this study, we investigated local populations of *R. alpina* and *M. a. funereus* in a forest reserve within Triglav National Park (Slovenia, Alpine biogeographical region). Using one-season field data from 12 suitable habitat patches, we focused on (i) patterns of occurrence in relation to tree characteristics as a measure of habitat preference, (ii) potential interspecific interactions arising from shared use of large-diameter trees, and (iii) baseline observations of demographic parameters.

MATERIAL AND METHODS

Study area and study plots

The study was conducted in the Lemovje forest reserve and adjacent protection forest in Triglav National Park, Slovenia. These forests are managed only minimally, with natural succession largely intact, and predominantly beech (*Fagus sylvatica*; > 70% of standing wood). The whole study area was thoroughly surveyed at the beginning of the study to identify suitable trees. Twelve habitat patches (HP I–XII, Fig. 1), each representing a study plot, were established between 926 and 1004 m above sea level (Table S1). Selection was based on the presence of at least one potentially suitable beech tree per plot (up to five, altogether 30 trees; see Table S1). Each plot was then spatially centred around these focal trees, which represented different stages of decay (hereafter referred to as "trunk condition"): (1) damaged: living tree with healthy leaves, mostly intact bark, and active cambium, though some minor visible damage (small broken branches, superficial bark injuries) may be present; (2) decaying: tree showing early to moderate signs of decay (partial leaf loss, some dead branches, bark loss, or cambium partially inactive); microhabitat structures may start to form (e.g. cavities, broken branches); (3) dead: tree with no living leaves and inactive cambium. Trunk, branches, or stumps may be partially or fully decayed, often with cavities, broken branches, or bark loss, providing microhabitats for saproxylic beetles. This includes standing, fallen dead trees, and stumps.

Plot coordinates and altitudes (Table S1), and coordinates of the inspected trees were recorded using a GPS (GPSMAP 66S, ± 3 m). The 12 habitat patches were arranged in a west to east direction, and distributed within an area of approximately 4.2 ha (42,000 m^2), based on the coordinates of habitat patch centres; maximum east–west extent ca. 680 m. Each plot measured approximately 2500 m^2, with a radius between 25 and 30 m. Distances among plots ranged from 30 to 680 m, with an average of 79.6 ± 28.6 m.

Field work

In 2020, we actively searched for *M. a. funereus* and *R. alpina* beetles during 13 sampling sessions from 7 July to 9 September at reasonably regular intervals (once or twice a week) in sunny and warm weather (air temperature > 20ºC) from 10 am to 4 pm regional time. We tried to adapt the frequency of sampling to the species studied, but weather conditions and the remoteness of the study sites also played an important role in the frequency of sampling. Since adults of *M. a. funereus* have a long life span (i.e. two years with an intermediate diapause: Drovenik & Pirnat, 2003; the whole life cycle lasts 3–4 years: Stanić et al., 1985; Luce, 1996), the time interval was well adapted to this species. However, the short average lifespan of *R. alpina* (up to 7 days; maximum lifespan: 15 and 35 days for females and males, respectively – Campanaro et al., 2017; the entire life cycle lasts at least 3 years, Drag et al., 2011) with its high dispersal ability (up to 1.6 km; Drag et al., 2011) could affect the efficiency of sampling. The average sampling interval (AVG ± SD = 5.33 ± 1.78 days) in our study was shorter than the maximum and average lifespan of *R. alpina*, so sampling efficiency was considered sufficient. We mainly searched for beetles on selected trees and stumps, as dead or freshly cut wood attracts xylophages, such as the two target species (Vrezec et al., 2008, 2009). Sampling effort was consistent: the same two people actively searched for beetles on each tree or stump for 10 min. We marked each animal found with a unique number on the left elytron, using permanent marker. We chose this approach to allow quick identification in the field. For each capture, we noted the sex of the animals, possible injuries to the antennae (only for live captures), and released them undamaged in the same place. We recorded the date and GPS coordinates (GPSMAP 66S; accuracy 3 m) for each initial or follow-up capture of each individual. Finally, the following parameters of the inspected sites and trees were recorded: location (site plots I–XII), altitude, exact GPS coordinates, trunk condition (dead versus dying = damaged and decaying conditions merged together due to scarce data), trunk position (fallen versus standing), trunk diameter at breast height, and sunlight exposure of the site and trunk.

Data analysis

Field observations were used to derive categorical predictors for subsequent analyses. Trunk diameter was classified into width categories based on diameter at breast height (DBH: 1 = 30–59 cm, 2 = 60–89 cm, 3 = 90–119 cm). Trunk illumination was categorised according to estimated sunlight exposure (in % of sunlight: 1 = < 50%, 2 = 50–69%, 3 ≥ 70%). Site illumination was classified as either predominantly shaded or predominantly sun-exposed (Table S1). Categorical variables, trunk width category and trunk illumination category, were used as numeric variables and centred and scaled prior to analysis. Due to the number of observations and the distance between sampling plots, we used location (coded as study plots) as a single explanatory variable rather than including longitude, latitude (both at plot and tree levels), altitude, or plot illumination status. Location and the remaining variables (trunk condition, trunk position, trunk width category, and trunk illumination category) were tested for multicollinearity using generalised variance inflation factors (GVIF; threshold = 2), as some predictors were categorical and others numeric (package car, Fox & Weisberg, 2019).

Abundance patterns for each species (all captures were included in the analysis) were modelled using zero-inflated negative binomial generalised linear mixed models (ZINB GLMMs) to account for overdispersion and excess zeros, with trunk condition, trunk position, centred trunk width category and centred trunk

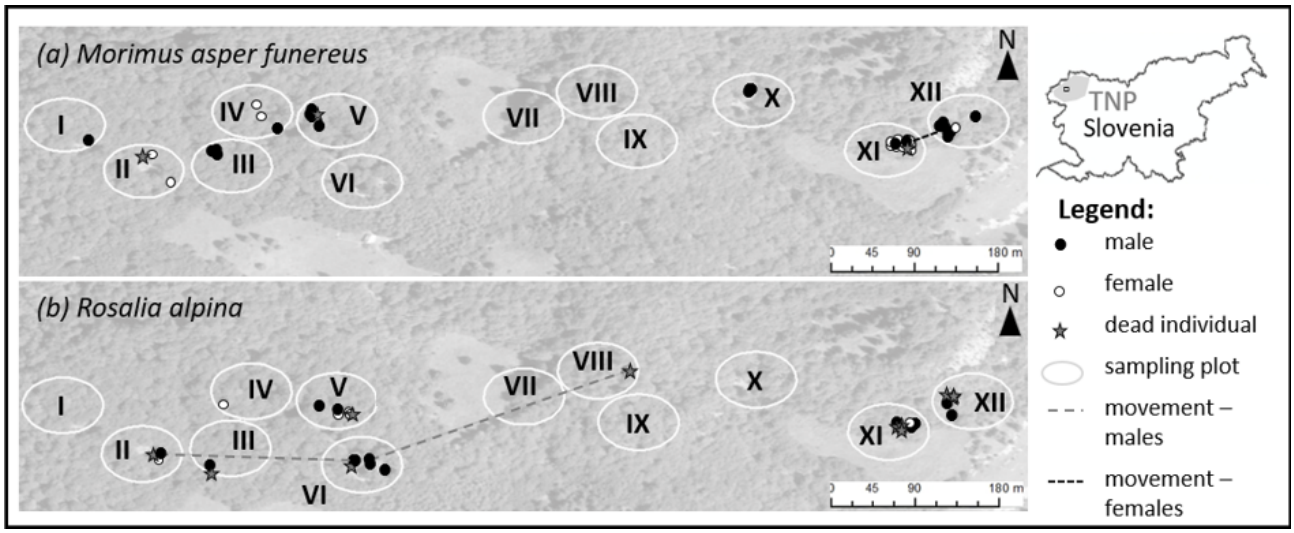

Fig. 1. Spatial distribution of captures of (a) *Morimus asper funereus* and (b) *Rosalia alpina* in the Lemovje forest reserve, Triglav National Park (TNP). The study area is indicated on the map of Slovenia (□). Sampling plots (ellipses, not to scale) are labelled with Roman numerals I–XII.

illumination category as fixed effects and location and date as random. Zero-inflation was modelled with ~1 to account for structural zeros. Potential interspecific competition was evaluated using binomial GLMMs with the presence of one species as a predictor of the other, controlling for the same trunk characteristics and random effects structure. Model assumptions were verified using DHARMa (Hartig, 2025) simulation-based residual diagnostics. This framework allowed us to assess microhabitat preferences and potential interspecific interactions between *M. a. funereus* and *R. alpina*, while acknowledging the limitations imposed by sample size and the field design. We also tested whether the effect of trunk width on *M. a. funereus* abundance differed among trunk conditions by including a trunk condition × trunk width interaction term in the model. All statistical modelling and plotting were performed in R version 4.3.2 (R Core Team, 2024) and run in RStudio 2025.9.1.401 (Posit Team, 2025) using the glmmTMB (Brooks et al, 2017), MuMln (Bartoń, 2025), DHARMa (Hartig, 2025), ggeffects (Lüdecke, 2018), and ggplot2 (Wickham, 2016) packages.

To estimate demographic parameters and population size, we tested closed and open population approaches in the program MARK 9.0 (White & Burnham, 1999) in the modules "Closed captures", "Cormack-Jolly-Seber" (CJS) and "POPAN" (Sandercock, 2020). However, we discarded closed population models due to a possible violation of closure (e.g. new individuals entering the population represented by births or other incoming individuals from other populations) and used only open population models (Chiari et al., 2013). We modelled the demographic parameters for the entire population of *M. a. funereus* (both sexes together). The individual marking of the beetles allowed us to create individual encounter histories (presence of the animal coded as "1" and absence as "0"), which were organised in the input file (.inp) and analysed in MARK. The "POPAN" formulation was used to model the demographic parameters of survival (φ), probability of capture (p) and recruitment rate (b), resulting in an estimate of the total population size (N). For the survival and capture probability parameters, we used three different parameterisations so that they could be constant (.), time-dependent (t) or with a linear trend (tlin), while we modelled recruitment in three different structures: as (t), (tlin) or (tlin + tlin^2), resulting in 27 different models. To estimate the goodness-of-fit of the global model (φ_t p_t), we performed the median c-hat test within the "CJS" module and used the resulting estimate to correct for overdispersion in the POPAN analysis. We then selected the best model according to the Akaike Information Criterion corrected for small sample size (AIC_c) (Burnham & Anderson, 2002), considering models with an $AIC_c < 2$. Given the sparse data on captured and especially recaptured individuals of *R. alpina*, the high mortality observed (see Table S2), and their predicted mobility, we were unable to model population size. We calculated the distances between successive captures of all animals that were recaptured at least once. The range of recorded distances was reported for both species. Movements were analysed in Excel 2016.

RESULTS

Within the system of 12 potentially suitable study plots (HP I–XII, Fig. 1), a total of 30 trees were examined for the presence of *M. a. funereus* and *R. alpina*. A total of 28 trees with different trunk conditions were occupied either by *M. a. funereus* (n = 18), *R. alpina* (n = 16) or both species (n = 6). In five study plots (I, VII–X), only one suitable tree was found, while in the other plots 2–5 suitable standing or fallen trees or their stumps were recorded (Table S1).

A total of 68 individuals (30 males and 38 females: 44.1% and 55.9%, respectively; 3 dead animals included) of *M. a. funereus* were found during 12 successful sampling sessions from 7 July to 4 September in 8 habitat patches (Tables S2 and S3). Most of them (88.2%) were found in plots XI (n = 34 individuals / 47 captures), XII (n = 13 / 17) and V (n = 13 / 16). No animals were found in plots VI–IX (Fig. 1). A total of 37 individuals of *R. alpina* were found in 8 habitat patches during 10 successful sampling occasions from 20 July to 9 September (Table S2). Out of 27 individuals found alive on the first capture, there were 18 (66.7%) males, and 9 (33.3%) females; a further 10 individuals (all on the last 3 occasions) were found dead on first capture and their sex was unidentifiable (Table S3). Most animals (83.7%) were found in plots XI (n = 10 individuals / 13 captures), XII (n = 10 / 10), V (n = 6 / 6), and VI (n = 5 / 6). No animals were found in plots I, VII, IX and X (Fig. 1).

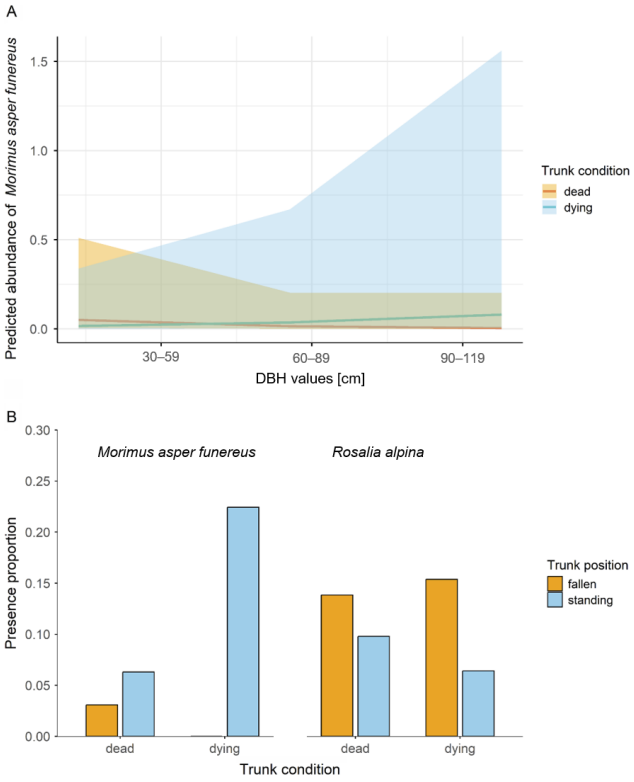

Fig. 2. Habitat use and interaction of *Rosalia alpina* and *Morimus asper funereus*. (A) Predicted abundance of *M. a. funereus* showing the interaction between trunk condition and trunk width categories. Lines indicate model predictions with 95% confidence intervals. *M. a. funereus* prefers dying trees and wider trunks, while illumination has no effect. (B) Presence proportion of *M. a. funereus* and *Rosalia alpina* (bars) across trunk conditions and positions. Bars are grouped by trunk condition.

In total, we collected 377 trunk-by-date observations. *R. alpina* was recorded 35 times, while *M. a. funereus* was recorded 46 times. All abundance pattern models met model assumptions, with no evidence of overdispersion, unexpected zero inflation, or non-random residual patterns. The model for *R. alpina* showed no strong predictors: there was a slight positive trend for trunk width category and a slight negative trend for standing trunks, but neither was significant ($p > 0.05$), indicating that *R. alpina* presence was patchy and mostly driven by location and date. In contrast, the model for *M. a. funereus* showed a strong preference for dying trunks (1.268 ± 0.477, $p = 0.008$) and for standing trunks (1.916 ± 0.860, $p = 0.026$; Fig. 2A). Trunk width category showed a marginal positive effect (0.404 ± 0.214, $p = 0.059$), while trunk illumination category had no detectable influence. The test of the model with the interaction of trunk condition × trunk width was significant for *M. a. funereus* ($\chi^2 = 6.064$, $df = 1$, $p = 0.014$), indicating that the increase in its abundance with trunk width was stronger on dying trunks than on dead trunks (Fig. 2A). No significant interaction was detected for *R. alpina*, consistent with its patchy presence. Mean *M. a. funereus* abundance and *R. alpina* presence proportion across trunk conditions and positions (Fig. 2B) illustrate their differing ecological preferences.

For the purposes of demographic modelling of *M. a. funereus*, we combined the last two successful sampling occasions (11th and 12th occasions: only 2 females and 1 male, respectively) into a single occasion, resulting in 11 occasions. The median c-hat test showed an overdispersion of the data with a c-hat = 1.35, which was used to correct the results in the POPAN analysis. Only one model was selected as best-fit, namely $\varphi_{tlin}\ p_{tlin}\ b_{tlin+tlin^2}$, with 8 parameters, while all other models had a ΔAICc of 3.6 or higher. Survival was high, but followed a linear downward trend, ranging from 0.975 (95% confidence interval 0.902–0.994) to 0.884 (95% CI 0.793–0.939) (see Table S4). Capture probability increased with a linear trend from 0.102 (95% CI 0.048–0.206) to 0.377 (95% CI 0.158–0.660) (Table S4); recruitment rate followed a parabola, with the highest recruitment recorded between 31 July and 6 August (sampling occasions 6 and 7) at 0.324 (95% CI 0.132–0.603) (Table S4). The total population size was estimated at 144 animals (95% CI 88–199). In total, 18 movements were recorded in males and 9 in females, with 92.6% of movements shorter than 3 m, i.e. the beetles stayed on the same tree. The maximum observed distance was 12 m in males and 34 m in females.

Out of 27 captures of live *R. alpina*, only 6 males were recaptured once (3 of which were dead recaptures), while females were not recaptured at all (Table S3). In addition, the 10 specimens that were found dead were clearly not previously marked. The distances between the three live recaptures were 5 m, 137 m and 215 m; for the additional three dead recaptured males the distances were 1 m, 2 m and 457 m.

DISCUSSION

In this study, we have demonstrated the importance of old beech forests with an abundance of dead, decaying or damaged trees and stumps for both beetle species. This tree species has already been described as very important for many saproxylic beetles, including both species in this study (Jurc et al., 2008; Leonarduzzi et al., 2017). The study area lies within the limits of the altitudinal distribution of the studied saproxylic beetles in Slovenia (*R. alpina*: 560–1540 m, Brelih et al., 2006; *M. a. funereus*: 150–1250 m, Vrezec et al., 2010). The simple method of inspecting dead and damaged trees in this area proved to be efficient, at least for *M. a. funereus* (see Vrezec et al., 2011; Rossi de Gasperis et al., 2016). However, a higher sampling frequency would result in a greater number of captures and perhaps allow detailed analyses of ecological and demographic parameters for both species (Sandercock, 2020).

We found a difference in the colonisation of different tree types between the two species. *M. a. funereus* showed a preference for still standing dying trees with wider trunks, while none of these microhabitat features proved to be significantly favoured by *R. alpina*. This suggests that *M. a. funereus* responds more strongly to combined habitat features, while *R. alpina* is less specialised, reinforcing the observation of distinct habitat preferences and reduced

direct competition. In contrast to our observations, Russo et al. (2011) reported that *R. alpina* prefers decaying but still standing trees with a sparser canopy, thicker bark, but not yet much undergrowth. For *M. a. funereus,* several studies showed conflicting ecological preferences; Polak (2012) reported avoidance of old, dry and barkless trees as well as older stumps (see also Romero-Samper & Bahillo, 1993; Drovenik & Pirnat, 2003; Chiari et al., 2013), whereas others have found no clear preference towards different tree categories (Campanaro et al., 2011; Bărbuceanu et al., 2015). However, spatial and ecological differences throughout the species' distribution area may play an important role in shaping specific local adaptations.

It should also be emphasised that different tree types may be favoured for different life functions of the two species. In the case of *M. a. funereus*, we often observed the presence of several beetles on larger, dying but still standing trees, where females can find suitable sites for oviposition (see Campanaro et al., 2011; Kariyanna et al., 2017), as such trunks may provide a more permanent habitat with sufficient food for their long development and better insulation from the decay conditions typical of forests with many dead trees (Jurc, 2004; Campanaro et al., 2011). Dead trees were rarely occupied by *M. a. funereus*; however, these were previously reported to be used by males as mating sites (Hardersen et al., 2017). Russo et al. (2011) reported that *R. alpina* could occupy a wide range of trees of different thicknesses, while Chiari et al. (2013) observed a higher probability of finding adult *M. asper* with increasing wood volume. While we found more animals on trees with larger diameters, the increased abundance with trunk diameter was pronounced in *M. a. funereus* ($p = 0.059$), but less evident in *R. alpina*, corroborating previous studies (Russo et al., 2011; Chiari et al., 2013).

Rare observations of both species at the beginning and end of the study period indicated most of the season was successfully covered. The rapid decline in abundance at the end of the season (Table S2) can be attributed to heavy rainfall (at some sites in the Julian Alps > 200 mm of precipitation on 29 and 30 August), which was accompanied by a substantial drop in temperature at the end of August 2020 (Cegnar, 2020). In this area, *M. a. funereus* appears to be more abundant than *R. alpina*. While a demographic analysis for *M. a. funereus* and a ranking of differently probable open population models were possible, we were unable to apply such models to the population of *R. alpina*, due to its low recapture rate and many dead animals (both marked and unmarked) found at the end of the study period, further supporting an open population. *M. a. funereus* exhibited a relatively high survival rate during the study period and a robust capture probability. An increase in the recruitment rate in early August can be attributed to the emergence of newly hatched adult beetles (Stanić et al., 1985; Polak, 2012). The MRR analysis estimated the adult population size at 144 adult individuals; however, at the time of the study a large part of the population was in the juvenile developmental stage, contributing to a significant increase in the total population size (cf. Drag et al., 2011). The relatively high apparent survival estimated for *M. a. funereus* is consistent with its limited dispersal ability due to its inability to fly (Drovenik & Pirnat, 2003; Rossi de Gasperis et al., 2016; Monné et al., 2017) and the high availability of suitable habitat within the forest reserve. Because apparent survival reflects both true survival and site fidelity, and cannot distinguish mortality from permanent emigration (White & Burnham, 1999), the observed values may reflect both favourable habitat conditions and reduced permanent emigration. Conversely, the lower recapture rate of *R. alpina* is more likely explained by its greater mobility and broader use of the surrounding forest than by lower survival alone (Drag et al., 2011). These contrasting demographic patterns therefore appear to reflect differences in life-history strategy rather than differences in habitat quality.

As some males of *M. a. funereus* display territorial behaviour (Polak, 2012) and stay on the same suitable tree for a long time, this is also reflected in their movements, which can be numerous and short in males, but much longer and less numerous in females (cf. Rossi de Gasperis et al., 2016). Since females of this species mate with several males during the season (Polak, 2012), they frequently move between trees in search of mating opportunities (Polak, 2012; Hardersen et al., 2017) and suitable trees for oviposition (Polak, 2012; Hardersen et al., 2017). This is also indicated by the higher recapture rate of males (cf. Chiari et al., 2013; Bărbuceanu et al., 2015).

Despite the low recapture rate of individuals from different patches, the connectivity within the study system could be indicated by at least a few movements of both species between the plots, probably ensuring gene flow between neighbouring local populations (Zimmermann et al., 2011; see also Jugovic et al., 2025). Unintentionally ignored suitable (micro)habitats between the studied plots further facilitate connectivity within the study system, which represents only a fraction of a larger contiguous forest reserve (Rugani & Diaci, 2012). The limited dispersal ability of *M. a. funereus* may explain why isolated suitable forest fragments are often not colonised by the species (Bărbuceanu et al., 2015). In remote habitat patches with few suitable trees, intraspecific competition for resources and mating opportunities leads to frequent *M. asper* male-male fights. Larger males reproduce more successfully, likely because they more often defeat smaller rivals (Rossi de Gasperis et al., 2018). As these fights involve the use of strong mandibles and can cause injuries, the high proportion of males with broken antennae observed in our study (Table S3) was expected. No such injuries were observed in the males of *R. alpina* (Table S3). The latter could be the result of the less pronounced territoriality of *R. alpina* (but see Duelli & Wermelinger, 2005). According to Drag et al. (2011), the dispersal ability of *R. alpina* is highly variable and depends on the spatial arrangement of suitable habitat. Individuals may remain predominantly within a habitat patch and move between suitable trees, but can also move considerable distances between habitat patches. Nevertheless, most individuals appear to stay within a few hundred metres of

their natal site (Drag et al., 2011). In our study system, such movements may additionally reflect the limited availability or prior occupation of suitable trees within habitat patches by *M. a. funereus*.

We also interpret the observed differences in habitat preference, demography, and mobility in the context of potential indirect competition between the two species. Although *M. a. funereus* and *R. alpina* are sympatric in the Lemovje Forest Reserve, they rarely occupied the same microhabitat (Table S5), suggesting spatial segregation and differences in habitat use and ecological niches. Both species are large-bodied saproxylic beetles that depend on coarse woody debris and large-diameter dead or dying trees for oviposition and larval development, resources that are spatially limited and heterogeneously distributed, particularly in managed forests. Several non-exclusive mechanisms may explain the observed differences in habitat use, including (1) species-specific habitat requirements; (2) context-dependent responses to local forest conditions (driven by local forest structure, microclimatic conditions, and the availability of suitable breeding substrates); (3) differences in dispersal ability and detectability (e.g. patchy distribution of *R. alpina* may partly reflect differences in detectability associated with its shorter adult lifespan and greater dispersal ability); or (4) temporal differences in adult activity and phenology. Resource partitioning and indirect competition represent one possible explanation, but the present data do not allow discrimination among these alternatives.

CONCLUSIONS

Our study demonstrates the importance of old-growth beech forests with abundant dead and dying wood for the persistence of *M. a. funereus* and *R. alpina* in the Lemovje Forest Reserve. The two species differed markedly in habitat use, demography, and dispersal behaviour. *M. a. funereus* showed a strong preference for large, standing, dying trees and exhibited predominantly short-distance movements, consistent with its limited dispersal ability and territorial behaviour. In contrast, *R. alpina* displayed broader and patchier habitat use together with greater mobility, including occasional long-distance movements between habitat patches. The high abundance and estimated population size of *M. a. funereus* indicate that the reserve currently provides favourable conditions for this species, while the low recapture rate of *R. alpina* suggests either lower local density or broader use of the surrounding continuous forest landscape. The observed differences in microhabitat use and movement patterns imply ecological niche differentiation, which may reduce direct competition between the two sympatric saproxylic beetles. Nevertheless, the possibility of indirect competition for large suitable trees cannot be excluded. Overall, our results emphasize the conservation value of unmanaged or minimally managed forest reserves with continuous availability of large-diameter dead and dying trees. Maintaining habitat continuity and structural heterogeneity is likely essential for sustaining viable populations and connectivity of saproxylic beetles in forest ecosystems.

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REFERENCES

Bărbuceanu D., Niculescu M., Boruz V., Niculescu L., Stoleriu C. & Ursu A. 2015: Protected saproxylic Coleoptera in "the Forests in the southern part of the Cândeşti Piedmont", a Romanian Natura 2000 Protected Area. — *Anal. Univ. Craiova (Ser. Agric. Mont. Cadast.)* **45**: 18–25.

Bartoń K. 2025: *MuMIn: Multi-Model Inference. R Package Ver. 1.48.11*. URL: https://CRAN.R-project.org/package=MuMIn

Brelih S., Drovenik B. & Pirnat A. 2006: Material for the beetle fauna (Coleoptera) of Slovenia. 2nd contribution: Polyphaga: Chrysomeloidea (= Phytophaga): Cerambycidae. — *Scopolia* **58**: 1–442 [in Slovenian, English abstract].

Brooks M.E., Kristensen K., van Benthem K.J., Magnusson A., Berg C.W., Nielsen A., Skaug H.J., Maechler M. & Bolker B.M. 2017: glmmTMB Balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. — *R Journal* **9**: 378–400.

Burnham K.P. & Anderson D. 2002: *Model Selection and Multi-Model Inference. A Pratical Information-Theoretic Approch.* Springer, New York, 488 pp.

Cálix M., Alexander K.N.A., Nieto A., Dodelin B., Soldati F., Telnov D., Vazquez-Albalate X., Aleksandrowicz O., Audisio P., Istrate P., Jansson N., Legakis A., Liberto A., Makris C., Merkl O., Mugerwa Pettersson R., Schlaghamersky J., Bologna M.A., Brustel H., Buse J., Novák V. & Purchart L. 2018: *European Red List of Saproxylic Beetles*. IUCN, Brussels, URL: https://portals.iucn.org/library/node/47296.

Campanaro A., Bardiani M., Spada L., Carnevali L., Montalto F., Antonini G., Mason F. & Audisio P. 2011: *Linee guida per il monitoraggio e la conservazione dell'entomofauna saproxilica.* Quaderni Conservazione Habitat 6, Cierre Grafica, Verona, 8 pp. + CD-ROM.

Campanaro A., De Zan L.R., Hardersen S., Antonini G., Chiari S., Cini A., Mancini E., Mosconi F., Rossi de Gasperis S., Solano E. & Bologna M.A. 2017: Guidelines for the monitoring of *Rosalia alpina*. — *Nature Conserv.* **20**: 165–203.

Cegnar T. 2020: Meteorology. — *Naše Okolje (Ljubljana)* **27**(8): 3–52 [in Slovenian].

Chiari S., Bardiani M., Zauli A., Hardersen S., Mason F., Spada L. & Campanaro A. 2013: Monitoring of the saproxylic beetle *Morimus asper* (Sulzer, 1776) (Coleoptera: Cerambycidae) with freshly cut log piles. — *J. Insect Conserv.* **17**: 1255–1265.

Council of Europe 1992: *Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora*. URL: http://eur-lex.europa.eu/

Danilevsky M.L. 2022: *A Check-list of Longicorn Beetles (Coleoptera, Cerambycoidea) of Europe*. pp. 1–40. URL: http://www.cerambycidae.net/europe.pdf (last accessed March 2024).

Drag L., Hauck D., Pokluda P., Zimmermann K. & Cizek L. 2011: Demography and dispersal ability of a threatened saproxylic beetle: a mark-recapture study of the Rosalia longicorn (*Rosalia alpina*). — *PLoS ONE* **6**: e21345, 8 pp.

Drovenik B. & Pirnat A. 2003: [*Expert Guidelines for the Establishment of the Natura 2000 Network: Beetles (Coleoptera): Final Report*]. Research Centre of the Slovenian Academy of Sciences and Arts, Jovan Hadži Institute of Biology, Ljubljana, pp. 71–80 [in Slovenian].

Dudley N. & Vallauri D. 2004: *Deadwood – Living Forests: The Importance of Veteran Trees and Deadwood to Biodiversity*. WWF, Gland, 19 pp.

Duelli P. & Wermelinger B. 2005: *Rosalia alpina* L.: A rare and emblematic cerambycid.). — *Sherwood* **114**: 19–25 [in Italian, English abstract].

Fernández-García J.M., Sesma J., Moreno E. & Mugarza V. 2023: Prioritizing forest patches to enhance habitat restoration and connectivity for the endangered saproxylic beetle *Rosalia alpina* (Coleoptera, Cerambycidae): a modelling approach. — *Munibe Cienc. Nat.* **71**: 67–69.

Fox J. & Weisberg S. 2019: *An R Companion to Applied Regression, 3rd ed*. Sage, Thousand Oaks, CA, URL: https://www.john-fox.ca/Companion/

Hardersen S., Bardiani M., Chiari S., Maura M., Maurizi E., Roversi P.F., Mason F. & Bologna M.A. 2017: Guidelines for the monitoring of *Morimus asper funereus* and *Morimus asper asper*. — *J. Nat. Conserv*. **20**: 205–236.

Hartig F. 2025: DHARMa: *Residual Diagnostics for Hierarchical (Multi-level / Mixed) Regression Models. R Package Version 0.4.7.* URL: https://github.com/florianhartig/dharma.

Jugovic J., Gorkič I. & Lužnik M. 2025: Population structure and habitat connectivity of *Phengaris teleius* (Lepidoptera: Lycaenidae) in southern Slovenia: Implications for conservation and landscape management. — *Eur. J. Entomol*. **122**: 229–241.

Jurc M. 2004: [The importance of saproxylic beetles and their conservation in Slovenia.] In Brus R. (ed.): [*Old and Thick Trees in the Forest: Collection of papers, XXII. Forestry Study Days*.] Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, pp. 57–74 [in Slovenian].

Jurc M. 2012: [Phytophagous entomofauna of beech forests of Slovenia.] In Bončina A. (ed.). [*Beech Forests in Slovena: Ecology and Management.*] Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, pp. 141–166 [in Slovenian].

Jurc M., Ogris N., Pavlin R. & Borkovic D. 2008: Forest as a habitat of saproxylic beetles on Natura 2000 sites in Slovenia. — *Rev. Ecol. (Terre Vie)* **63**: 53–66.

Kariyanna B., Mohan M. & Gupta R. 2017: Biology, ecology and significance of longhorn beetles (Coleoptera: Cerambycidae). — *J. Entomol. Zool. Stud.* **5**: 1207–1212.

Kostova R., Bekchiev R., Popgeorgiev G. & Kornilev Y.V. 2023: First exhaustive distribution and habitat modelling of *Morimus asper* (Sulzer, 1776) sensu lato (Coleoptera, Cerambycidae) in Bulgaria. — *Nature Conserv.* **53**: 39–59.

Leonarduzzi G., Onofrio N., Bardiani M., Maurizi E., Zandigiacomo P., Bologna M.A. & Hardersen S. 2017: Attraction of different types of wood for adults of *Morimus asper* (Coleoptera, Cerambycidae). In Campanaro A., Hardersen S., Sabbatini Peverieri G. & Carpaneto G.M. (eds): Monitoring of saproxylic beetles and other insects protected in the European Union. — *Nature Conserv.* **19**: 135–148.

Luce J.-M. 1996: *Morimus funereus* Mulsant, 1863. In van Helsdingen P.J., Willemse L. & Speight M.C.D. (eds): *Background Information on Invertebrates of the Habitats Directive and the Bern Convention. Part I – Crustacea, Coleoptera and Lepidoptera.* Nature and Environment No. 79, Council of Europe Publishing, Strasbourg, pp. 59–63.

Lüdecke D. 2018: ggeffects: tidy data frames of marginal effects from regression models. — *J. Open Source Softw.* **3**: 772, 5 pp.

Monné M.L., Monné M.A. & Wang Q. 2017: General morphology, classification, and biology of Cerambycidae. In Wang Q. (ed.): *Cerambycidae of the World: Biology and Pest Management.* Taylor & Francis, Boca Raton, pp. 1–70.

Müller J., Bussler H. & Kneib T. 2008: Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. — *J. Insect Conserv.* **12**: 107–124.

Polak S. 2012: Phenology and mating behaviour of *Morimus funereus* (Coleoptera, Cerambycidae). In Jurc M. (ed.): *Saproxylic Beetles in Europe: Monitoring, Biology and Conservation.* — *Studia Forest. Sloven.* **137**: 43–52.

Posit Team 2025: *RStudio: Integrated Development Environment for R*. Posit Software, PBC, Boston, MA, URL: http://www.posit.co/

R Core Team 2024: *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, URL: https://www.R-project.org/

Ranius T. 2002: Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. — *Biol. Conserv.* **103**: 85–91.

Romero-Samper J. & Bahillo P. 1993: Some observations on the distribution and biology of *Morimus asper* (Sulzer, 1776) (Coleoptera: Cerambycidae) in the Iberian Peninsula. — *Bol. Asoc. Esp. Entomol*. **17**: 103–122 [in Spanish, English abstract].

Rossi de Gasperis S., Passacantilli C., Redolfi De Zan L. & Carpaneto G.M. 2016: Overwintering ability and habitat preference of *Morimus asper*: a two-year mark-recapture study with implications for conservation and forest management. — *J. Insect Conserv*. **20**: 821–835.

Rossi de Gasperis S., Redolfi De Zan L., Romiti F., Hardersen S. & Carpaneto G.M. 2018: Sexual dimorphism and allometry of secondary sexual character in *Morimus asper* (Coleoptera: Cerambycidae). — *Zoomorphology* **137**: 119–130.

Rugani T. & Diaci J. 2012: [Beech primeval forests in Slovenia: structure and development dynamics.] In Bončina A. (ed.): [*Beech Forests in Slovenia: Ecology and Management.*] Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, pp. 193–207 [in Slovenian].

Russo D., Cistrone L. & Garonna A. 2011: Habitat selection by the highly endangered long-horned beetle *Rosalia alpina* in Southern Europe: a multiple spatial scale assessment. — *J. Insect Conserv.* **15**: 685–693.

Sandercock B.K. 2020: Mark-recapture models for estimation of demographic parameters. In Murray D.L. & Sandercock B.K. (eds): *Population Ecology in Practice*. Wiley-Blackwell, Oxford, pp. 157–190.

Solano E., Mancini E., Ciucci P., Mason F., Audisio P. & Antonini G. 2013: The EU protected taxon *Morimus funereus* Mulsant, 1862 (Coleoptera: Cerambycidae) and its western Palaearctic allies: systematics and conservation outcomes. — *Conserv. Gen.* **14**: 683–694.

Speight M.C.D. 1989: *Saproxylic Invertebrates and Their Conservation*. Nature and Environment Series No. 42, Council of Europe, Strasbourg, 79 pp.

Stanić V., Ivanović J., Janković-Hladni M., Nenadović V. & Marović R. 1985: Feeding habits, behaviour, oviposition and longevity of the adult cerambycid beetle *Morimus asper funereus* Muls. (Col., Cerambycidae) under laboratory condition. — *Acta Entomol. Jugoslav.* **21**: 87–94.

Stokland J.N., Siitonen J. & Jonsson B.G. 2012: *Biodiversity in Dead Wood.* Cambridge University Press, Cambridge, NY, 524 pp.

Vrezec A., Pirnat A., Kapla A. & Denac D. 2008: [*The Design of Monitoring the State of Populations of Selected Target Species of Beetles, Including Supplementing the Proposal for Areas to be Included in the NATURA 2000 Network:* Morimus funereus, Rosalia alpina, Cerambyx cerdo, Osmoderma eremita, Limoniscus violaceus, Graphoderus bilineatus.] National Institute of Biology, Ljubljana, 101 pp. [in Slovenian].

Vrezec A., Ambrožič Š., Polak S., Pirnat A., Kapla A. & Denac D. 2009: [*Implementation of Monitoring of the State of Populations of Selected Target Species of Beetles in 2008 and 2009 and Design of Monitoring of the State of Populations of Selected Target Species of Beetles.* Carabus variolosus, Leptodirus hochenwartii, Lucanus cervus, Morimus funereus, Rosalia alpina, Bolbelasmus unicornis, Stephanopachys substriatus, Cucujus cinnaberinus, Rhysodes sulcatus.] National Institute of Biology, Ljubljana, 174 pp. [in Slovenian].

Vrezec A., Ambrožič Š. & Kapla A. 2010: Biology and ecology of flightless cerambycid *Morimus funereus* (Mulsant, 1862) as a background for monitoring application: laboratory and large-scale field study. In Jurc M., Repe A., Meterc G. & Borkovič D. (eds): *Book of Abstracts. 6th European Symposium and Workshop on Conservation of Saproxylic Beetles, June 15–17, 2010, Ljubljana*. University of Ljubljana, p. 20.

Vrezec A., Pirnat A., Kapla A., Polak S., Vernik M., Brelih S. & Drovenik B. 2011: Status and knowledge about beetles (Coleoptera) of European conservation importance in Slovenia with proposal of Slovenian nomenclature. — *Acta Entomol. Sloven.* **19**: 81–138 [in Slovenian, English abstract].

White G.C. & Burnham K.P. 1999: Program MARK: survival estimation from populations of marked animals. — *Bird Study (Supl.)* **46**: S120–S139.

Wickham H. 2016: *ggplot2: Elegant Graphics for Data Analysis.* Springer, New York, pp. 3–10.

Zimmermann K., Blazkova P., Cizek O., Fric Z., Hula V., Kepka P., Novotny D., Slamova I. & Konvicka M. 2011: Demography of adults of the Marsh fritillary butterfly, *Euphydryas aurinia* (Lepidoptera: Nymphalidae) in the Czech Republic: Patterns across sites and seasons. — *Eur. J. Entomol.* **108**: 243–254.

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Table S1. Summary table of the plots with the number of beech trees examined based on the trunk conditions (DYING = damaged + decaying, DEAD = dead + stump) and categorised as standing or fallen. For each tree category, the number of animals detected/captured (*M.a.f.* – *Morimus asper funereus*, and *R.a.* – *Rosalia alpina*) is given. Alt – altitude in metres above sea level. X, Y – GPS coordinates of study plots. Abbreviations for sun exposure at plot level (S.e.): sh – predominantly shaded, ex – predominantly sun exposed. Abbreviations for the status of trees in categories 1–3: S – standing, F – fallen.

Plot	Alt	X, Y	S.e.	DYING						DEAD					
				Damaged			Decaying			Dead			Stump		
				No. trees	*M.a.f.*	*R.a.*	No. trees	*M.a.f.*	*R.a.*	No. trees	*M.a.f.*	*R.a.*	No. trees	*M.a.f.*	*R.a.*
I	984	46°21′03.35″ N 13°40′21.05″ E	ex	0	/	/	1^{S}	1	0	0	/	/	0	/	/
II	972	46°21′01.67″ N 13°40′23.81″ E	ex	0	/	/	1^{S}	1	0	1^{F}	1	4	1	1	0
III	988	46°21′02.94″ N 13°40′25.95″ E	sh	0	/	/	1^{F}	0	2	0	/	/	1	9	0
IV	1004	46°21′03.64″ N 13°40′28.24″ E	sh	1^{S}	1	0	0	/	/	2^{S} + 1^{F}	2	1	0	/	/
V	999	46°21′03.51″ N 13°40′30.59″ E	sh	0	/	/	2^{S}	15	0	1^{S} + 1^{F}	1	3	1^{S}	0	3
VI	978	46°21′01.29″ N 13°40′31.47″ E	sh	0	/	/	0	/	/	1^{S}	0	2	2^{S}	0	4
VII	957	46°21′03.66″ N 13°40′37.12″ E	ex	0	/	/	0	/	/	1^{F}	0	0	0	/	/
VIII	965	46°21′04.56″ N 13°40′39.70″ E	ex	0	/	/	0	/	/	1^{S}	0	2	0	/	/
IX	950	46°21′02.77″ N 13°40′41.11″ E	sh	1^{S}	0	0	0	/	/	0	/	/	0	/	/
X	955	46°21′04.25″ N 13°40′45.20″ E	sh	1^{S}	2	0	0	/	/	0	/	/	0	/	/
XI	931	46°21′02.63″ N 13°40′50.44″ E	ex	0	/	/	2^{S}	47	11	1^{F}	0	2	0	/	/
XII	926	46°21′03.26″ N 13°40′52.92″ E	ex	0	/	/	4^{S}	17	4	1^{F}	0	6	0	/	/
TOTAL				3	3	0	11	81	17	11	4	20	5	10	7

Table S2. Summary of the number of males and females of *M. a. funereus* and *R. alpina* caught in NW Slovenia on 13 occasions in July, August and September 2020. For *R. alpina*, the number of individuals of undetermined sex is also given. The number of additional dead animals found is given in brackets. *The 11th and 12th sampling occasions were combined into a single occasion for analysis in MARK.

Sampling occasion	1	2	3	4	5	6	7	8	9	10	11*	12*	13
Date	7.7.	10.7.	14.7.	20.7.	27.7.	31.7.	6.8.	14.8.	18.8.	21.8.	27.8.	4.9.	9.9.
Interval (days)		3	4	6	7	4	6	8	4	3	6	8	5
M. a. funereus													
Males	1	5	9	6	3	3	6	4	6	4	0	1	0
Females	6	3	6	6	3	2 (+1)	10	4	5	0 (+2)	2	0	0
Total	7	8	15	12	6	6	16	8	11	6	2	1	0
R. alpina													
Males	0	0	0	1	1	1	3#	2	4	5	3 (+1)	0 (+2)	1
Females	0	0	0	0	1	3	2	0	0	2	0	0	1
Undetermined	0	0	0	0	0	0	0	0	0	0	0 (+3)	0 (+3)	0 (+4)
Total	0	0	0	1	2	4	5	2	4	7	7	5	6

This number includes one individual that was recorded twice in the same day on different trees.

Table S3. Summary of data on the number of males and females of *M. a. funereus* and *R. alpina* caught during our study in NW Slovenia. For *R. alpina*, the number of individuals of undetermined sex is also given. The number of additional dead animals found is given in brackets. *One third of marked *M. a. funereus* individuals (n = 10) had visible antennae injuries; #No *R. alpina* individuals exhibited injured antennae (n = 0).

Species	Sex	No. of marked individuals	No. of recaptured individuals	% of recaptured individuals	No. of captures	No. of recaptures	% of recaptures
	Males	30*	9	30.0	48	18	37.5
M. a. funereus	Females	38	7 (+2)	23.7	50	9 (+3)	24.0
	Total	68	18	26.5	98	30	30.6
R. alpina	Males	18#	3 (+3)	33.3	24	3 (+3)	25.0
	Females	9	0	0.0	9	0	0.0
	Undetermined	10	0	0.0	10	0	0.0
	Total	37	6	16.2	43	6	13.9

Table S4. Estimates of demographic parameters (p – capture probability, φ – survival, b – recruitment, N_i – daily population sizes) with 95% confidence intervals (CI) of Morimus asper funereus from Triglav National Park (Slovenia) in 2020. # – sampling occasion. The estimates are based on the selected best model ($\varphi_{tlin}\ p_{tlin}\ b_{tlin+tlin^2}$). Estimates for φ and b are shown at the beginning of consecutive time intervals.

#	Date	p Estimate (CI)	φ Estimate (CI)	b Estimate (CI)	N_i Estimate (CI)**
1	7.7.	0.1029 (0.0483–0.2060)			90 (55–147)
2	10.7.	0.1193 (0.0631–0.2141)	0.9750 (0.9016–0.9940)	0 (0–0)	84 (53–131)
3	14.7.	0.1380 (0.0805–0.2264)	0.9681 (0.9108–0.9890)	0 (0–0)	73 (48–111)
4	20.7.	0.1590 (0.0988–0.2458)	0.9603 (0.9141–0.9822)	0 (0–0)	58 (38–88)
5	27.7.	0.1825 (0.1158–0.2756)	0.9518 (0.9128–0.9738)	0 (0–0)	41 (25–67)
6	31.7.	0.2086 (0.1296–0.3183)	0.9424 (0.9068–0.9649)	0.0002 ($3.2\ 10^{-6}$–0.0101)	32 (18–56)
7	6.8.	0.2374 (0.1397–0.3739)	0.9323 (0.8951–0.9569)	0.3242 (0.1315–0.6031)	68 (39–118)
8	14.8.	0.2688 (0.1468–0.4400)	0.9214 (0.8772–0.9506)	0.0485 (0.0013–0.6659)	42 (27–66)
9	18.8.	0.3028 (0.1519–0.5129)	0.9098 (0.8536–0.9458)	$6\ 10^{-7}$ (0–0.0020)	29 (17–49)
10	21.8.	0.3390 (0.1556–0.5800)	0.8974 (0.8251–0.9420)	0 (0–0)	21 (11–39)
11	31.8.*	0.3772 (0.1584–0.6608)	0.8844 (0.7928–0.9387)	0 (0–0)	6 (2–18)

*The 11th and 12th sampling occasions on 27th August and 4th September, respectively, were combined into a single occasion (denoted as 31st August); **Truncated to the nearest full number.

Table S5. Spatial and temporal coincidence of *M. a. funereus* and *R. alpina* (number of captures) on 28 occupied trees, shown by tree diameter. *Dead *M. a. funereus* found on the same day on the same tree as a living *R. alpina*.

Tree diameter (cm)	*M. a. funereus*	*R. alpina*	Temporal coincidence
33	1	0	No
37	1	1	No
53	0	2	No
54	1	0	No
56	0	2	No
58	0	1	No
58	0	2	No
64	1	0	No
65	9	0	No
65	0	3	No
66	1	4	1* *M. a. f.* + 1 *R. a.* (31. 7.)
70	1	0	No
71	0	2	No
72	3	0	No
75	0	1	No
77	2	0	No
78	0	2	No
84	1	0	No
85	20	8	2 *M. a. f.* + 1 *R. a.* (31. 7.)
90	1	0	No
90	1	0	No
90	12	0	No
91	0	3	No
95	0	6	No
101	1	0	No
101	10	3	3 *M. a. f.* + 1 *R. a.* (6. 8.)
102	5	1	No
115	27	3	5 *M. a. f.* + 2 *R. a.* (6. 8.)