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Cucujus cinnaberinus (Scopoli, 1763) at its *terra typica* in Slovenia: historical overview, distribution patterns and habitat selection

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Abstract

The saproxylic beetle, *Cucujus cinnaberinus,* has received increasing research attention in Europe since the adoption of the Habitats Directive and establishment of the Natura 2000 network. The history of the species has been investigated as well as the influence of abiotic and biotic variables on the distribution of *C. cinnaberinus* in Slovenia which is at the limit of its range and also *terra typica* for the species. The species was first described in 1763 by Joannes A. Scopoli in Carniola, a duchy of the Habsburg Monarchy. Today, most of the territory of Carniola is situated within Slovenia. *C. cinnaberinus* is particularly common in the eastern part of the country, but very scarce in the mountainous western part. According to historical and recent distribution patterns of *C. cinnaberinus* in the former Carniolan territory, the region of Ribnica-Kočevje in southern Slovenia is proposed as the most probable type locality of the species. Although the bulk of the *C. cinnaberinus* population in Slovenia is confined to the lowlands, the species has been found up to 1095 m a.s.l., albeit at a much lower abundance due to the influence of climate and forest structure. Although *C. cinnaberinus* is a quite an opportunistic species regarding host tree selection, it has been shown to exhibit a preference for *Tilia, Populus* and *Robinia*. It is suspected that the high abundance of *C. cinnaberinus* in lowland floodplain forests is due to the recent human-induced increase in preferred fast-growing and short-lived host trees, i.e. the planting of poplar trees and spread of invasive Black Locust (*Robinia pseudoacacia*) after the 1960s. In contrast, in montane forests, preferred host trees (e.g. *Tilia*) represent < 1 % of all growing stock. Although montane *C. cinnaberinus* populations are rare, they could still be important for the conservation of the species, since montane habitats cover the largest area within the species' distribution range.

Keywords
saproxylic beetle, Natura 2000, type locality, Carniola, altitudinal distribution, host tree selection, macrohabitat, large-scale survey

Introduction

The Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora or the Habitats Directive (92/43/EEC) was adopted in 1992 and subsequently spurred intensive research activity on species of conservation concern in Europe. This is particularly evident with respect to the saproxylic beetles which is amongst the most threatened beetle groups in Europe (Nieto and Alexander 2010) and is reflected in the number of published papers listed in the Web of Science on 21 saproxylic beetle species of conservation concern, with 87 % of all papers published after the year 1992 and, in particular after 2010, when more than 50 % of all papers were published. However, research activity has been skewed towards more widespread and charismatic species (e.g. Ranius et al. 2005, Harvey et al. 2011), at least that concerning species ecology, monitoring, distribution and conservation biology (see Appendix: Table S1).

There are only four well studied species in this sense, namely *Osmoderma eremita, Morimus funereus, Lucanus cervus* and *Rosalia alpina* and three moderately studied species *(Cucujus cinnaberinus, Cerambyx cerdo, Limoniscus violaceus)*, while the majority of species have been poorly studied or not studied at all. While this deficiency in research greatly hampers the conservation management of Natura 2000 sites, on the other hand, it stimulates applied research on species survey methods, monitoring and conservation management (e.g. Bussler and Müller 2009, Carpaneto et al. 2010, Harvey et al. 2011, Bergman et al. 2012, Gouix and Brustel 2012, Chiari et al. 2013, Walentowski et al. 2013, Gough et al. 2014, Le Gouar et al. 2015, Campanaro et al. 2016, Carlsson et al. 2016, Hopkins and Thacker 2016, Larsson 2016).

Until recently, *Cucujus cinnaberinus* was considered as a poorly known species (Horák 2011). It is confined to Europe and is distributed from the Mediterranean to Scandinavia and from Russia to Spain, but with a scattered distribution pattern, probably due to past population decline and local extinctions (Horák and Chobot 2009, Horák et al. 2010). The species has however an extremely cryptic lifestyle, as the larvae and adults live under the bark of dead tree trunks (Horák et al. 2008) and this might also be a reason for the low detection rate of the species in the past (Horák et al. 2010).

Recently, field survey techniques have shifted from focusing on adult beetles to the detection of larvae under the bark which appears to be a much more efficient detection method (Bussler 2002, Straka 2006, Vavra and Drozd 2006, Horák and Chobot 2011, Vrezec et al. 2012, Gutowski et al. 2014). By applying the larval survey technique, new discoveries of the species have accelerated, as have rediscoveries in regions where the species was previously thought to be extinct (Mazzei et al. 2011, Kovács et al. 2012, Fuchs et al. 2014, Holly 2014, Mainda 2014, Hörren and Tolkiehn 2016, Šag et al.

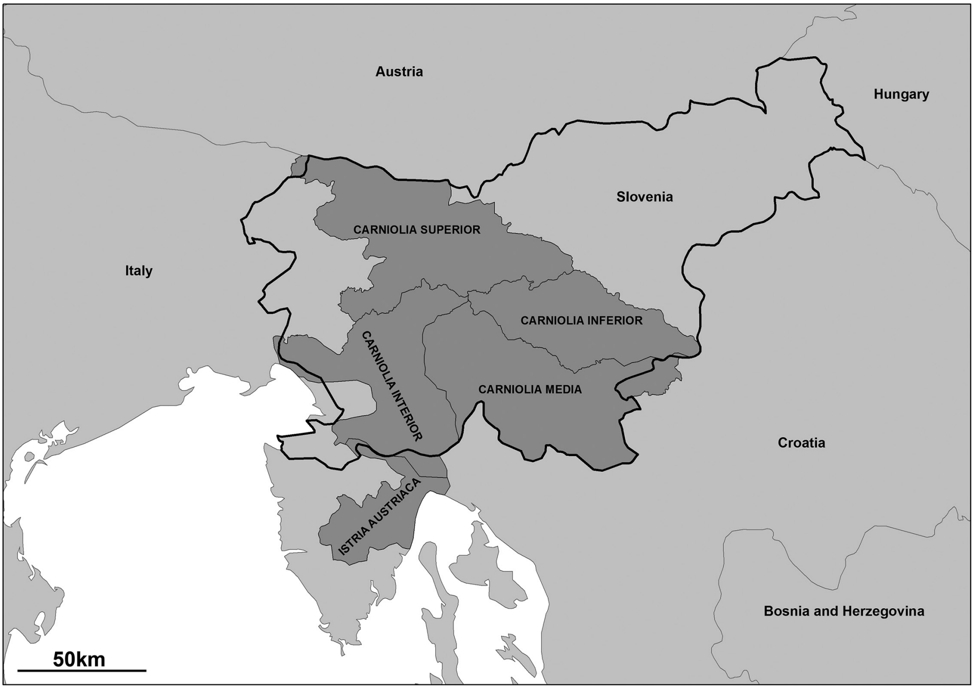

Figure 1. The Duchy of Carniola (dark grey) in the period of Joannes A. Scopoli's research activity between 1754 and 1769 with Carniolan provinces marked with their original Latin names. Recent state borders in the region are marked in the background. The map was redrawn after Florjančič de Grienfeld (1744).

2016, Tovar and Baena 2016). This intensified research activity uncovered new records of other *Cucujus* species and led to the discovery of a new endemic species in Europe (Horák et al. 2009, 2011, Bonacci et al. 2012, Gutowski et al. 2014). Horák et al. (2008, 2010) claimed that the *C. cinnaberinus* population stronghold is situated in central European countries, although this might change due to increasing knowledge on species distribution and abundance in southern Europe (Mazzei et al. 2011, Vrezec et al. 2011, Kovács et al. 2012, Šag et al. 2016).

In 1763, Joannes A. Scopoli described the species as *Meloe Cinnaberinus* from Carniola (also Carniolia, Krain, Kranjska), a duchy of the Habsburg Monarchy. Today, most of the Carniolan territory is situated within Slovenia (Figure 1), where the type specimen originated (Scopoli 1763). This fact has however been largely neglected in recent papers (e.g. Horák and Chobot 2009, Horák et al. 2010, Bonacci et al. 2012) partly as a result of the lack of knowledge about the type locality of *C. cinnaberinus* (i.e. the Duchy Carniola was frequently misinterpreted in the past; Baker 1999) which was not specifically mentioned in the original description of Scopoli (1763) and partly as a result of lack of knowledge on the recent status of *C. cinnaberinus* in the former Carniolan territory and the current Slovenian territory (Pirnat and Drovenik 2004, Horák et al. 2010, Vrezec et al. 2011). Therefore, the aim of this paper was to review historical and recent knowledge about the distribution of *C. cinnaberinus* in its *terra* *typica* in Slovenia, with special emphasis on J. A. Scopoli's research activity in the region (Petkovšek 1977, Baker 1999, Štih et al. 2008), in order to identify the most probable type locality of the species. As *C. cinnaberinus* is highly genetically polymorphic (Røed et al. 2014), it is essential to define the type locality as a population reference for further taxonomic and phylogenetic studies of this and related species.

Taking into account recent distribution maps of *C. cinnaberinus* (Horák et al. 2008, Horák and Chobot 2009), it seems that Slovenia represents the limit of the species' distribution since there is no population known in the western neighbourhood of Northern Italy (Brandmayr et al. 2016). This situation presents the opportunity to study the species' micro- and macrohabitat selection patterns at the edge of its distribution, where it is rarer and less abundant. So far, the species' habitat parameter associations have been intensively studied only in central Europe, in its population stronghold where it is very abundant and its population is even expanding (Horák et al. 2010, 2011). This study therefore aimed: (1) to assess horizontal and vertical distribution patterns of *C. cinnaberinus* in Slovenia at its distribution edge, based on large-scale field sampling guided by a potential distribution model; (2) to review historical data of species occurrence in Slovenia from 1763 onwards and (3) to determine species macro- and microhabitat selection patterns to assess the limitation parameters of the species' distribution at the edge of its range.

Methods

Study area

The study was conducted over the whole territory of Slovenia (20,273 km^2) which is a predominantly montane country with more than one-third of the surface lying above an elevation of 600 m a.s.l. (Perko and Orožen Adamič 1998). With forests covering 58 % of its area, Slovenia is one of the most forested European countries (Slovenia Forest Service 2015). Despite forest exploitation being an important economic activity, Slovenia has largely managed to preserve the original forest communities and populations of indigenous trees, even in some areas with a large amount of deadwood (Slovenia Forest Service 2015). The prescribed amount of deadwood biomass left in the forest varies up to 3 % of the total wood stock in the stands (Uradni list RS 2009, 2016).

The dominant tree species is European Beech (*Fagus sylvatica*), forming the most frequent forest associations of *Fagetum, Abieti-Fagetum* and *Querco-Fagetum* in Slovenia (70 %; Slovenia Forest Service 2015). Most of the western part of the country is montane with prevailing tree species of European Beech, Silver Fir (*Abies alba*), Norway Spruce (*Picea abies*), European Larch *(Larix decidua)*, Sweet Chestnut *(Castanea sativa)* and Sessile Oak *(Quercus petraea)* (Perko and Orožen Adamič 1998). In eastern Slovenia, the forest has been mainly preserved where land is less suitable for agriculture and in floodplains along major river banks (Mura, Drava, Sava and Krka). They are characterised by a large volume of deadwood; for example, in the floodplain forest along the

Mura River, it ranges from 15 to 24 m^3/ha (Ferreira and Planinšek 2016). The prevailing species in floodplain forests are Common Alder (*Alnus glutinosa*), Pedunculate Oak (*Quercus robur*), Willow (*Salix* sp.), Poplar (*Populus* sp.; including hybrid Poplars) and European Hornbeam (*Carpinus betulus*) (Perko and Orožen Adamič 1998). Intensive plantations of hybrid poplars were established in the period from 1960–1980 (Božič and Krajnc 2012). Plantations were established on alluvial sites along the main rivers in Slovenia (Drava, Krka, Mura, Sava, Savinja, Soča) with primarily native poplar and willow stands. Additionally, Black Locust (*Robinia pseudoacacia*) is the most widespread alien tree species in Slovenia and accounts for almost two-thirds of the growing stock of non-native tree species (Kutnar and Kobler 2013).

Only part of Slovenia belonged to the former Duchy of Carniola which existed in the former Holy Roman Empire and later in the Habsburg Monarchy between 1364 and 1918 (Kos 1929, Štih et al. 2008). According to recent state borders in the region, the territory of Carniola is located in Slovenia, except for a small part that is included within the current borders of Italy and Croatia (Figure 1). In the period of J.A. Scopoli's research activity in Carniola between 1754 and 1769 (Petkovšek 1977), the duchy was divided into five regions: northern Carniola Superior (today, Gorenjska, including the mountainous area of the Julian Alps), western Carniola Interior (today, Notranjska and part of Primorska, including the northern part of the Dinaric karst region), eastern Carniola Inferior and Media (today, Dolenjska, extending to the river banks of the Sava and Krka and including the current major forest complexes in southern Slovenia) and Istria Austriaca (NE part of Istria and mainly within the current territory of Croatia) (Florjančič de Grienfeld 1744, Brelih et al. 2006).

According to *Flora Carniolica* (Scopoli 1760, 1772) and *Entomologia Carniolica* (Scopoli 1763), J. A. Scopoli began researching the flora and fauna of Carniola shortly after his arrival in Idrija with the first surveys in the year 1755 (Petkovšek 1977). To demonstrate the study area of Scopoli in the territory of the former Duchy of Carniola, we took into account all known localities visited by Scopoli and mentioned in his major works (Scopoli 1760, 1763, 1772, Petkovšek 1977, Baker 1999, Štih et al. 2008) with a circular area of a 10 km radius around every locality. The overlap of all historical and recent records of *C. cinnaberinus* within Scopoli's study area was used as a guideline in defining the possible type locality from which the Scopoli (1763) type specimen originated. Scopoli's collection with his type specimens is most probably lost (Brelih et al. 2006).

Historical *Cucujus cinnaberinus* range assessment

Data on the past distribution of *C. cinnaberinus* in the territory of Slovenia were obtained from literature reviews (Brelih 2001, Drovenik and Pirnat 2003) and by examination of historical entomological collections of coll. Ferdinand Jožef Schmidt (period between 1819 and 1878; stored in Slovenian Museum of Natural History in Ljubljana-PMSL), coll. Josip Stussiner (end of the 19th and beginning of the 20th century; stored in PMSL), the Central Collection of Slovenian beetles (collection curated by Savo Brelih with material originated from coll. A. Bianchi, S. Brelih, E. Jaeger and J. Peyer from the period between the end of the 19th century to 2012; stored in PMSL), coll. Josef (Giuseppe) Müller (first half of the 20th century; stored in Museo Civico di Storia Naturale, Trieste), coll. Jože Staudacher (period between 1918 and 1940; stored in PMSL), coll. Alfonz Gspan (period between 1918 and 1940; stored in PMSL) and coll. Egon Pretner and Božidar Drovenik (period between 1920 and 2010; stored at Research Centre of the Slovenian Academy of Sciences and Arts, Ljubljana). All historical records were accidental findings since no systematic surveys of the species were known before the year 2008 (Vrezec et al. 2009). Historical records were geolocated at a scale of 10 kilometres and were used only for the purpose of horizontal distribution analysis in this study.

Recent assessment of *Cucujus cinnaberinus* distribution patterns

In Slovenia, the first large-scale surveys of *C. cinnaberinus* started in 2008 (Vrezec et al. 2009) by searching for larvae under the bark of dead trees (Straka 2006, Vavra and Drozd 2006, Vrezec et al. 2012). From the sites from where no adult beetles were obtained, the larvae were taken to the laboratory and reared to verify species identification. The procedure of rearing larvae in the laboratory until they reached the adulthood was the same as described in Gutowski et al. (2014). From most of the sites, voucher specimens were preserved. Surveys were directed towards the areas from which historical data existed (Brelih 2001, Drovenik and Pirnat 2003) and towards the floodplain forests which were reported as the main *C. cinnaberinus* habitat in central Europe (Straka 2006, Horák et al. 2008, Schlaghamersky et al. 2008).

In the period 2008–2011, 944 geolocated data items (deadwood inspections and occasional findings) were collected. In 53 of those, *C. cinnaberinus* presence was confirmed, including lowland as well as montane populations. However, assessing the distribution range of rare and elusive species is difficult, especially when historical data are scarce, this usually being the case for species with a cryptic lifestyle due to past methodological and knowledge limitations. In saproxylic beetles, potential distribution models have proved to be an essential tool for species distribution assessments and for designing targeted field surveys (Thomaes et al. 2008, Ranius et al. 2011, Bosso et al. 2013).

In a previous study, this approach was applied to assess the potential distribution of *C. cinnaberinus* in the territory of Slovenia based on available data until 2011 as a guideline for a further large-scale field study (Vrezec et al. 2014). The data were used to construct spatial models by a machine learning process resulting in the assembly of a model based on 100 regression trees. From the model of potential habitat suitability, the theoretical distribution model for 0.70 and 0.50 probability of species occurrence (Figure 2) was extracted. On this basis, further surveys were designed focusing on the most promising areas for the species in the country between 2012 and 2016, taking

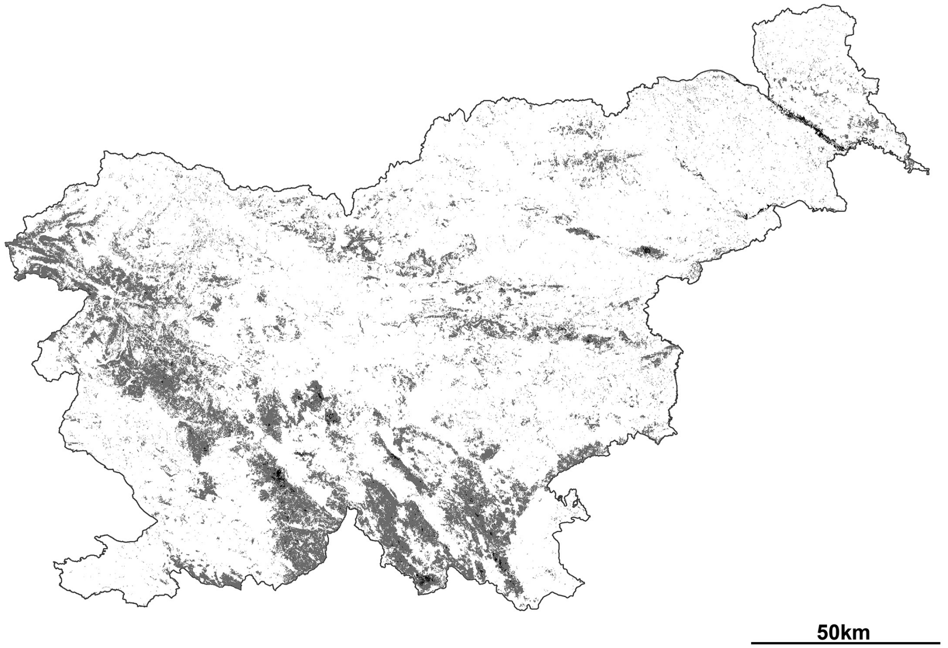

Figure 2. The theoretical distribution model of *Cucujus cinnaberinus* in Slovenia based on the sites with 0.70 (black areas) and 0.50 (grey areas) probability of species occurrence according to the potential habitat suitability model based on the data set collected in the period 2009–2011 (Vrezec et al. 2014). The model was used as a guideline for a large-scale species survey in the period 2012–2016.

into account the whole territory of Slovenia with lowland and montane habitats. The technique of searching for larvae under the bark of dead trees was applied in all areas. The abundance index of the species was estimated as a percentage of inspected trees with confirmed *C. cinnaberinus* presence.

Microhabitat analysis

During field surveys, microhabitat characteristics of inspected dead tree trunks were recorded (i.e. tree species, diameter and length of the trunk). Although dead tree trunks were investigated throughout the whole of Slovenia, only the locations where *C. cinnaberinus* presence was confirmed were included in further microhabitat analysis. To describe *C. cinnaberinus* host tree preferences, a modified version of Ivelev's electivity index D (Jacobs 1974) was used. In further analysis, only trees with 25 or more observations were included (*Alnus, Fraxinus, Populus, Quercus, Robinia, Salix* and *Tilia*). For analysis of microhabitat data, a generalised linear model (GLM) with binomial error distribution was used (McCullagh and Nelder 1989). The independent variable was the absence and presence of the larvae or imago of *C. cinnaberinus* under the bark of sampled trunks. The independent variables were tree species and the diameter and length of the inspected tree trunk. With the variable diameter of the sampled dead tree trunk, a nonlinear relationship was detected. Therefore, the quadratic variable of the diameter of the tree trunk was added to the model (Zuur et al. 2010). Furthermore, the variable was log + 1 transformed, because outliers were detected. Records with incomplete data for any of the variables were deleted. Model selection was performed on the basis of stepwise backwards selection using the χ^2 test (McCullagh and Nelder 1989). When the variable did not significantly add to the model, the variable was dropped.

Macrohabitat analysis

For analysis of the macrohabitat of *C. cinnaberinus*, all collected geolocated field data in the period 2009–2016 were used and data points were described with variables of deadwood stock, altitude, amount of deciduous tree wood stock, canopy cover and solar radiation. The deadwood was sampled on 724 and 746 plots dispersed in a 4 × 4 km^2 grid over the whole of Slovenia by the Slovenian Forestry Institute in 2007 and 2012, respectively (Slovenian Forestry Institute 2016).

To assess the variables at each *C. cinnaberinus* survey point, all the plots in a radius of 10 km around the survey point were taken into account. The deadwood stock (m^3/ha) per survey point was averaged over time and space within a 10 km radius. With this approach, a robust dataset for a longer period within 10 km of the location of the sampled tree trunk for *C. cinnaberinus* was created. The wood stock of deciduous trees (m^3/ha) and the canopy cover for every sampling site were assessed at the stand level and obtained from the Slovenian Forest Service database (Slovenia Forest Service 2015).

The canopy cover was divided into four classes: dense canopy closure (canopy very dense, branches deformed), normal canopy closure (branches meet each other, branches not deformed), sparse canopy closure (canopy very open, branches of neighbouring trees do not meet when windy) and patchy canopy closure (the gap may be one or more tree crowns) (Slovenia Forest Service 2015). The altitude and slope were extracted from the digital elevation model of Slovenia (Surveying and Mapping Authority of the Republic of Slovenia 2010). The annual solar radiation was obtained from GIS layers of annual solar radiation for the whole Slovenia (Zakšek et al. 2005, Kastelec et al. 2007).

For the analysis of macrohabitat selection, a GLM with binomial error distribution was used. The dependent variable was the presence and absence data of the larvae of *C. cinnaberinus*. The independent variables were slope, altitude, wood stock of deciduous trees, canopy cover, solar radiation and deadwood stock. The wood stock of coniferous trees was not included since it was the inverse of the wood stock of deciduous trees (Vrezec et al. 2014). The deadwood was transformed with a log + 1 transformation. The altitude and the amount of deciduous trees were transformed with a square root transformation. This was undertaken because outliers were detected. Model selection was performed in a similar way to the microhabitat analysis. The analysis was done in the programme R (R Development Core Team 2011).

Results

Cucujus cinnaberinus distribution in Slovenia: the historical and recent situation

In total, 365 records of *C. cinnaberinus* were collected in Slovenia in the period from 1763 to 2016. The majority of the records (96 %) were however found after the year 2008, when a systematic survey involving the larval search method was initiated (Figure 3; Vrezec et al. 2009). All larvae reared in the laboratory to adult beetles were found to belong only to the *C. cinnaberinus* species. Recent surveys in higher-elevation montane and low-elevation floodplain forests revealed that the abundance of the species was much larger in the latter ($\chi^2 = 32.6$, df = 1, $p < 0.001$), with the bulk of the population confined to lower elevations, although the species was found to be distributed in a large altitudinal span from 140–1095 m a.s.l. (Table 1, Figure 4).

In contrast, before 2008, the majority of the records were from high-elevation montane forests which is opposite to the recent situation ($\chi^2 = 456.1$, df = 1, $p < 0.001$; Table 1). Records before 2008 were all occasional findings of single adult beetles scattered around Slovenia (Figure 5), but none of them originated from the recently identified large *C. cinnaberinus* population in floodplain forests alongside the large Slovenian rivers of the Mura, Drava and Sava (Figure 6). The species' populations showed a maximum concentration and abundance of individuals in the eastern part of the country in

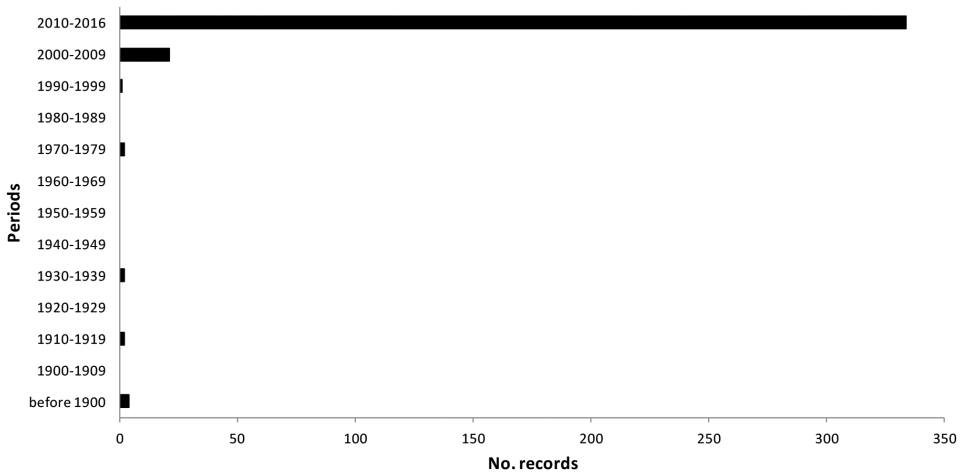

Figure 3. Number of records of *Cucujus cinnaberinus* per period in Slovenia from 1763 to 2016 (N=365). The last century is subdivided into decades.

Table 1. Proportion of records of *Cucujus cinnaberinus* in Slovenia found in two forest types in two time periods and occupancy rate of dead host trees in each forest type (only locations with confirmed species presence were included in the calculation of the occupancy rate).

Forest type	1916–2007 (N=6 records)	2008–2016 (N=354 records)	Occupancy rate: MIN–MAX (Median) (N=904 inspected trees, 9 locations)
Higher-elevation montane forests	88 %	7 %	2.0–10.2 % (3.8 %)
Lower-elevation floodplain forests	12 %	93 %	9.6–45.5 % (12.6 %)

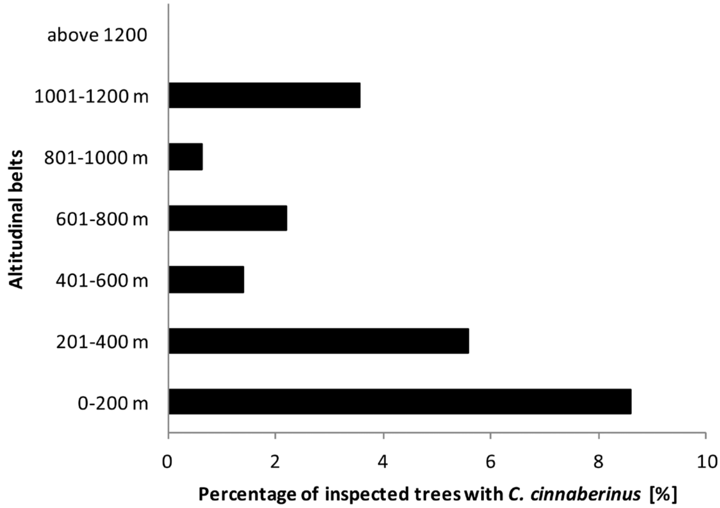

Figure 4. Altitudinal distribution of *Cucujus cinnaberinus* in Slovenia (N = 2132 inspected trees).

the lowlands, while its abundance and number of sites gradually decreased towards the western and mountainous part of Slovenia (Figure 6).

The oldest record for *C. cinnaberinus* in Slovenia was obtained in the period from 1755 to 1763; the specific collection site was not reported (Scopoli 1763). According to historical and recent data of *C. cinnaberinus* within the territory of the former Duchy of Carniola, four regions of species occurrence can be identified (from west to east; Figure 7): the Branica River Valley, Mt. Snežnik, the Ribnica-Kočevje region and the lower Sava River by Brežice. Although Scopoli obtained zoological and botanical material from many parts of the former Duchy of Carniola, only a few sites overlap with the known records of *C. cinnaberinus*: the region of former Carniola Media, today the Ribnica-Kočevje region in southern Slovenia and Carniola Interior and the Branica River Valley in the western part of Slovenia (Figure 7). A review of historical and recent data showed that abundance was low in both areas, but much higher in the Ribnica-Kočevje region on the mountains of Velika Gora, Stojna, Kočevski Rog and Stružnica. From here, the species was reported at least twice in the 20th and 21st century and also

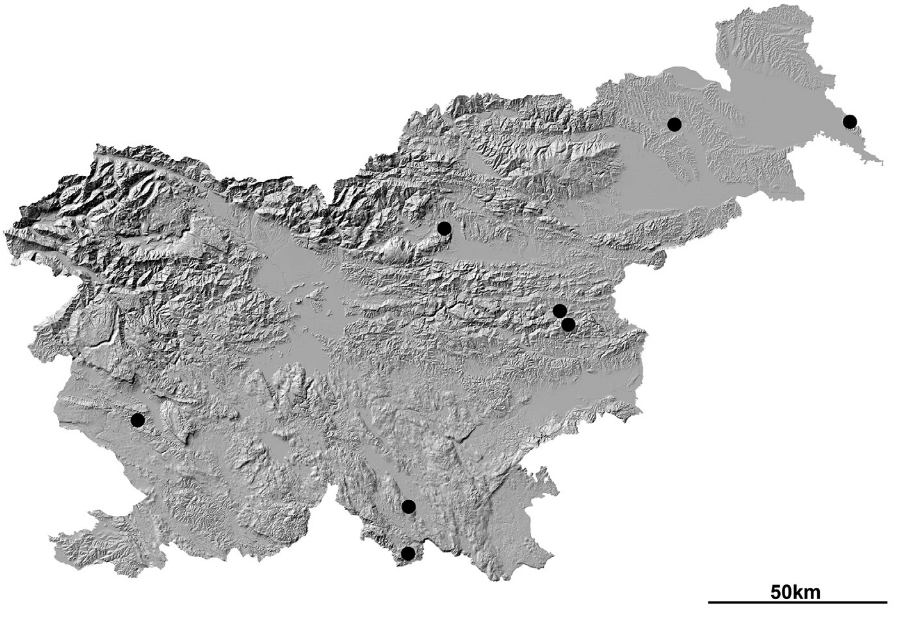

Figure 5. Distribution of historical records of *Cucujus cinnaberinus* in the period 1916–2002 in Slovenia before the introduction of the larval search method in 2008.

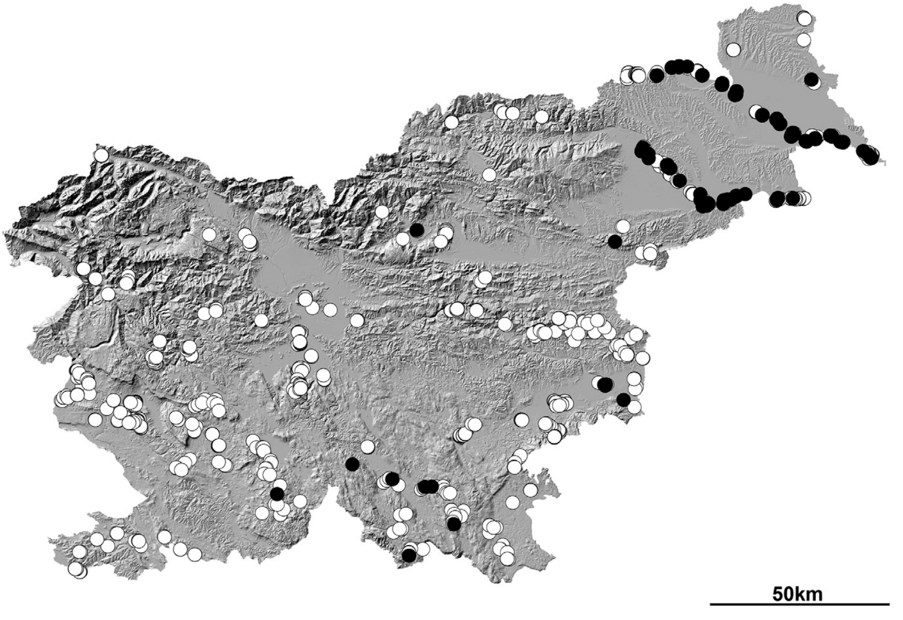

Figure 6. Results of a large-scale survey of *Cucujus cinnaberinus* in Slovenia conducted in the period 2008–2016. Black dots are species occurrence records (N=354) and white dots are sites of inspected dead tree trunks without confirmation of the species (N=2013).

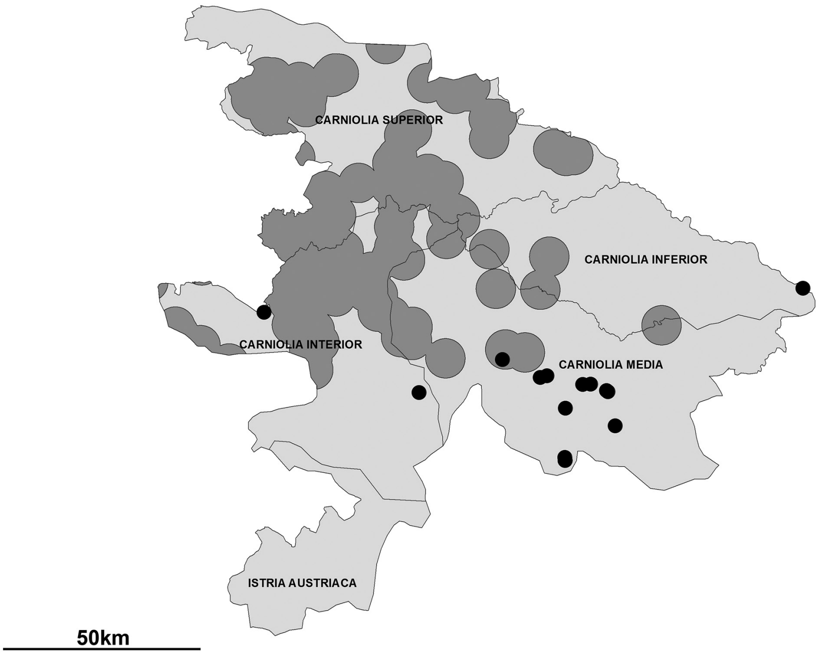

Figure 7. The Duchy of Carniola with the estimated study area of J. A. Scopoli in the period 1755–1763 (dark grey area) with all known historical and recent records of *Cucujus cinnaberinus* (black dots).

confirmed at seven sites in the large-scale survey in the period 2008–2016 in 10 % of all inspected trees in the region (Figure 6). In contrast, at the western location in the Branica River Valley, only one report from 2002 is known (Drovenik and Pirnat 2003) and the species was subsequently not found despite intensive surveys (N=239 inspected trees) in the period 2008–2016 (Figure 6). Mt. Snežnik produced a similar pattern, where *C. cinnaberinus* was only recently found in extremely low abundance in only 2 % of inspected trees. In contrast, the species was recently found to be very abundant in poplar plantations around the lower Sava River near Brežice, with 45 % of inspected trees being occupied by *C. cinnaberinus*, there being no evidence that Scopoli obtained material from the easternmost part of Carniola. From the 19th century, only three specimens of *C. cinnaberinus* were known to have been found in Slovenia and are preserved in the collection of F. J. Schmidt (PMSL), dating between 1819 and 1878, with no exact date and location specified. The first accurate records are from 1916 and 1918 and were found in a montane forest near Planina pri Sevnici by Dr Arthur Hoschek von Mühlheim (coll. A. Gspan in PMSL). Until 2008, before the large-scale survey of the species, *C. cinnaberinus* was known from a total of eight locations and, in at least three of these locations, the species was not reconfirmed despite systematic inspection of dead tree trunks for larvae (Figure 5 and 6).

Table 2. Host tree preferences of *Cucujus cinnaberinus* with the proportion of available trees, proportion of occupied trees and modified Ivelev's electivity index (D). D>0 signifies host trees preferred by *C. cinnaberinus*. (N=834 trees)

Host tree	Proportion of available trees in the sample	Proportion of occupied trees in the sample	D
Tilia	0.030	0.076	0.452
Robinia	0.073	0.118	0.256
Populus	0.237	0.328	0.220
Acer	0.013	0.017	0.122
Ulmus	0.023	0.025	0.052
Quercus	0.067	0.067	0.001
Salix	0.337	0.286	-0.119
Prunus	0.025	0.017	-0.203
Fraxinus	0.056	0.025	-0.396
Abies	0.020	0.008	-0.421
Alnus	0.097	0.034	-0.511
Fagus	0.011	0.000	-1.000
Betula	0.004	0.000	-1.000
Picea	0.004	0.000	-1.000
Pinus	0.002	0.000	-1.000

Table 3. Generalized Linear Model statistics of the best model for the microhabitat of *Cucujus cinnaberinus*.

Variables	Estimate	Std. Error	z value	Pr (>|z|)
(Intercept)	-5.57	0.86	-6.47	9.78E-11
Fraxinus	0.01	0.80	0.02	0.986
Populus	1.25	0.55	2.26	0.024
Quercus	0.54	0.68	0.80	0.424
Robinia	1.66	0.61	2.72	0.007
Salix	0.69	0.56	1.24	0.213
Tilia	2.00	0.68	2.95	0.003
Trunk length < 2 m	-0.57	0.50	-1.15	0.250
Trunk length > 5 m	1.06	0.28	3.77	0.000
Diameter (cm)	0.69	0.22	3.19	0.001

Microhabitat selection patterns

C. cinnaberinus was collected in 11 host tree genera, with *Salix* being the most frequently occupied host tree species and which was also the most frequent in the samples of all inspected trees. However, *Tilia, Robinia* and *Populus* were largely preferred and selected in a much larger proportion than were actually represented (Table 2). The model revealed that the host tree and the length and diameter of the inspected tree trunk were the most important variables explaining the probability of *C. cinnaberinus* presence (Table 3, Fig-

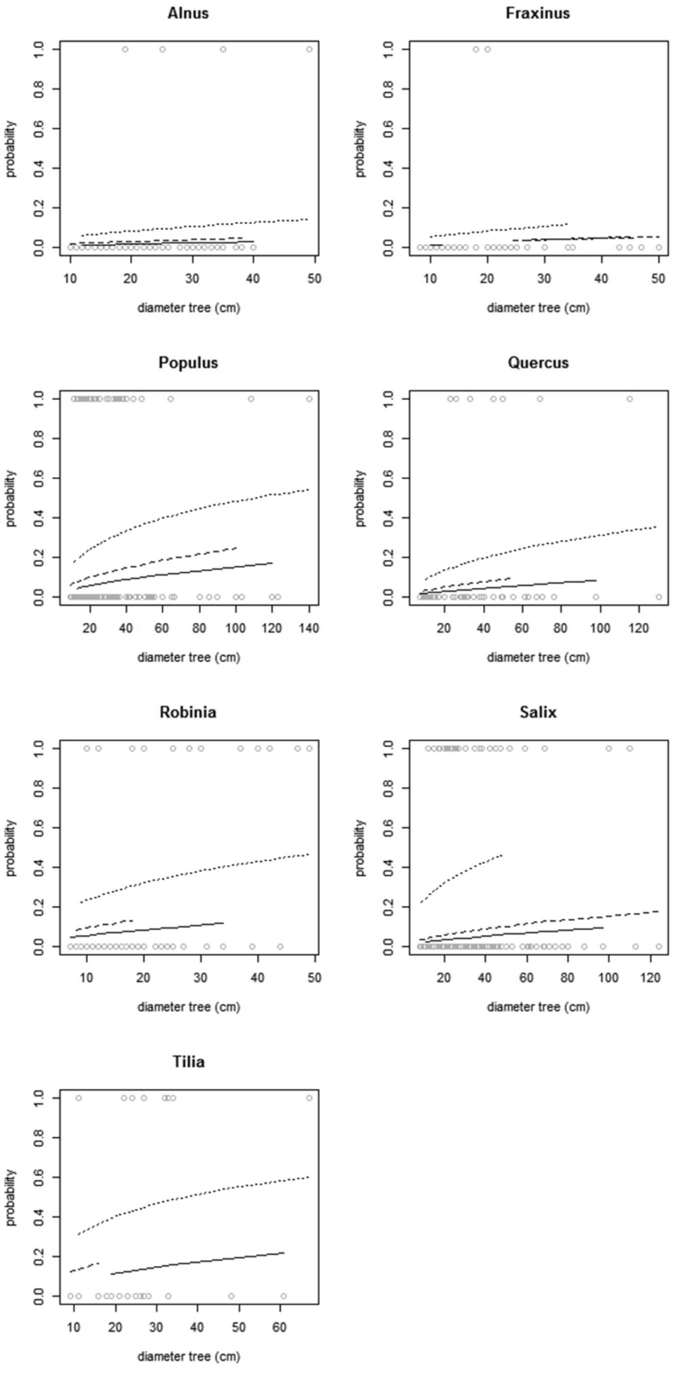

Figure 8. Predicted probability of occurrence of *Cucujus cinnaberinus* depending on the host tree and the diameter and length of the tree trunk. The solid line represents a tree length below 2 m, the dashed line represents trees between 2 and 5 meters long, and the stippled line represents trees longer than 5 m. The empty circles show the presence (1.0) and absence (0.0) of *C. cinnaberinus* in relation to diameter.

Table 4. Generalized Linear Model statistics of the best model for the macrohabitat of *Cucujus cinnaberinus*. Canopy closure classes were compared to the "dense canopy closure" class.

Variables	Estimate	Std. Error	z value	Pr (>|z|)
(Intercept)	-3.36	0.82	-4.11	3.88E-05
Altitude	-0.09	0.03	-3.51	0.00
Amount of deciduous trees	0.07	0.03	2.46	0.01
Amount of deadwood	0.28	0.13	2.16	0.03
Normal canopy closure	-0.12	0.52	-0.24	0.81
Sparse canopy closure	0.73	0.50	1.47	0.14
Patchy canopy closure	0.92	0.53	1.72	0.09

ure 8). The AUC of the model was 0.74 and, therefore, the model explained a fair share of the gathered data. The host tree largely influenced *C. cinnaberinus* colonisation and was of high importance (ΔAIC to model without variables = 12.9). Longer dead tree trunks had a higher probability of being colonised by *C. cinnaberinus* and were of high importance (ΔAIC to model without variables = 31.4). Additionally, *C. cinnaberinus* showed a higher preference for trunks with a larger diameter.

Macrohabitat selection patterns

For the macrohabitat, the best model included altitude, the amount of deadwood and the openness of the canopy (Table 4, Figure 9). Elevation showed a significant negative relationship with the probability of *C. cinnaberinus* colonising a tree. Both the amount of deciduous trees and amount of deadwood had a positive effect on colonisation probability. Canopy openness in general showed an increasing probability from closed canopy to open canopy. The model had an AUC of 0.72 which showed that the model predicts a fair share of the observed data.

Discussion

This study revealed that, within the former Duchy of Carniola, where *C. cinnaberinus* was described for the first time (Scopoli 1763), there are at least four regions that may represent the species' type locality. It is known however that J. A. Scopoli obtained zoological and botanical material for his studies from only two of these regions (Petkovšek 1977, Baker 1999): the Branica River Valley near Vipava and the montane forests of the Ribnica-Kočevje region. The review of *C. cinnaberinus* records showed that the beetle was present in moderate abundance only in the Ribnica-Kočevje region in the past and recent records show a similar pattern. It is known that J. A. Scopoli himself visited the region around Ribnica several times, especially in the autumn when he collected mushrooms (Petkovšek 1977). Additionally, he obtained material,

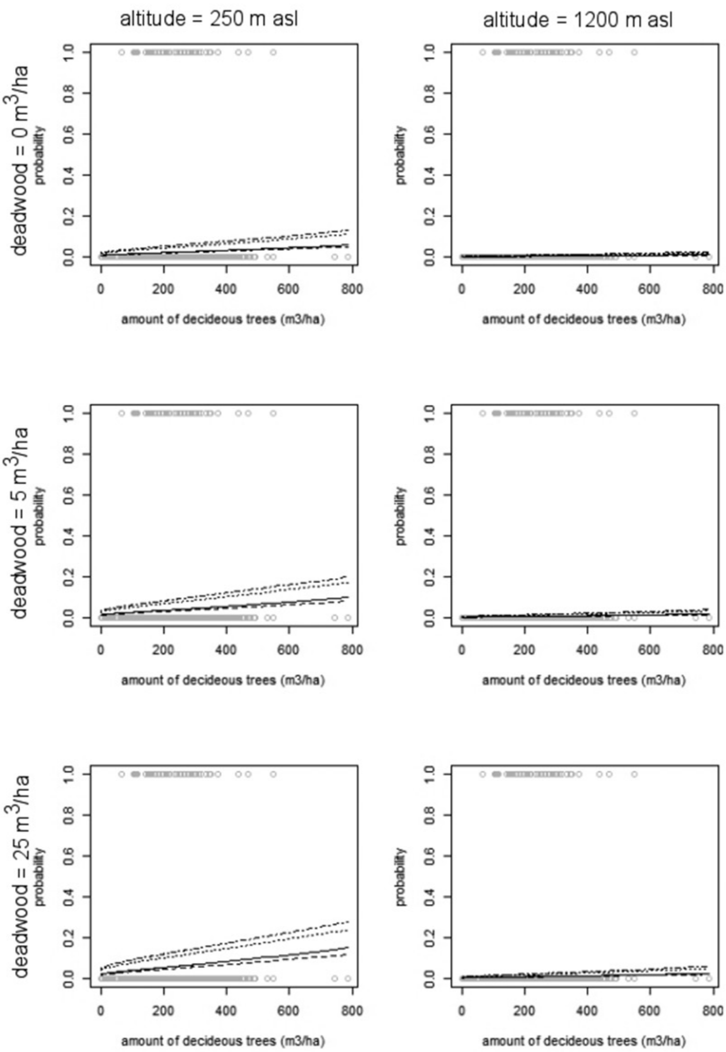

Figure 9. Predicted probability of occurrence of *Cucujus cinnaberinus* depending on altitude, amount of deciduous trees, amount of deadwood and openness of canopy cover. The solid line shows dense canopy closure; the dashed line shows normal canopy closure; the stippled line shows sparse canopy closure; the dashed-stippled line shows patchy canopy closure. Particular values were taken from altitude (median and maximum values) and amount of deadwood (minimum, median and maximum values) to emphasize the influence of different variables on each other and on the probability of colonization of tree trunks by *C. cinnaberinus*. The empty circles show the presence (1.0) and absence (0.0) of *C. cinnaberinus* in relation to the amount of deciduous trees.

predominantly plants, from the vicinity of Kočevje from a colleague Franz Xaver von Wulfen (Scopoli 1772, Petkovšek 1977). In his description of *C. cinnaberinus*, Scopoli (1763) noted "Octobri M. in *Brassica oleracea* capitata repertus & adlatus", meaning that "The species was found on a cabbage head and brought to him in mid October". Since *C. cinnaberinus* is a strict saproxylic species living under the bark of dead trees and with a limited flight season in spring and also in autumn (Horák and Chobot 2011), it is argued that the discovery of the specimen on a cabbage plant suggests only an occasional finding of a single specimen. It is very unlikely that such a finding would be recorded where the species is extremely rare such as in the Branica River Valley where only one record exists from 2002 and where the species was not confirmed again in later intensive surveys. The area is apparently the westernmost limit of the species distribution in SE Europe since there is no record known for the species further to the west in northern Italy (Horák and Chobot 2009, Brandmayr et al. 2016). Conversely, in the Ribnica-Kočevje region, *C. cinnaberinus* was reported in historical surveys (in 1930s and 1970s) as well as in recent surveys after 2008 at a moderate trunk occupancy rate of 10 %. Therefore, it is proposed that the Ribnica-Kočevje region in southern Slovenia with Mts. Velika gora, Stojna, Kočevski Rog and Stružnica are the most probable type locality for *C. cinnaberinus*. Despite intensive field studies, no other *Cucujus* species has been recorded in Slovenia neither recently nor in the past and this may decrease the possibility of misinterpretation of Scopoli's specimen as an identity of *C. cinnaberinus*.

Throughout the 19th and 20th century, *C. cinnaberinus* was considered as an extremely rare species in Slovenia with few known records and a similar pattern was suspected in other parts of Europe (see literature review in Horák et al. 2010). However, even large populations could have gone undetected due to the species' elusive behaviour and sparse distribution or due to ineffective survey procedures (McDonald 2004). The latter was particularly evident in *C. cinnaberinus*, with a dramatic recent increase in records after application of the larval search method and the pattern over the last century is remarkably similar in Slovenia as well as in other countries (Horák et al. 2010, Eckelt et al. 2014). Moreover, this type of data increase is expected in most of the beetle species listed in the Habitats Directive due to an increase in research after the Directive's adoption (see Introduction for literature review). The results from this study and reports of new discoveries of *C. cinnaberinus* populations in many countries across Europe (see Introduction for literature review) are not in accordance with the interpretation of Horák et al. (2010) that rarity and species absence, especially in southern European countries, is a result of population extinctions or decline in the past, but rather it is a consequence of research deficiency and overlooked populations. A Europe-wide study evaluating the population status of *C. cinnaberinus* and taking into account abundance estimates and research efforts to reveal species distribution and its population strongholds is thus needed. It was confirmed that the observations of Horák et al. (2010) about species population strongholds being limited to lignicultures and riparian forest stands including stands of fast growing invasive alien trees such as Black Locust *(Robinia pseudoacacia)* also hold true in southern Europe. Surprisingly, there were no historical records for *C. cinnaberinus* known from these sites in Slovenia which might support the hypothesis that the recent population expansion is due to a change in the structure of riparian forests due to intensifying poplar lignicultures and spread of invasive non-native tree species (Horák et al. 2010, Eckelt et al. 2014, Fuchs et al. 2014, Hörren and Tolkiehn 2016). In Slovenia, this was particularly true in lowland floodplain forests, in which there was intensive poplar planting in the period from 1960–1980 (Božič and Krajnc 2012) and rapid expansion of the Black Locust which regionally had already reached more than 6 % of the growing stock in the forests (Kutnar and Kobler 2013). Nevertheless, *C. cinnaberinus* was found in a wide altitudinal range from the lowlands up to 1095 m a.s.l. in Slovenia, up to 1400 m a.s.l. in Austria (Eckelt et al. 2014) and even above 1500 m a.s.l. in Albania (Kovács et al. 2012). The field study based, on a preliminary species distribution model, revealed that higher elevation montane forest stands could represent a significant part of the species' distribution range by surface area, although, in these habitats, the species was much less abundant than in the lignicultures and riparian forests of the lowlands.

Due to low abundance, there have been few studies actually reporting the species from montane habitats (e.g. Holzer and Friess 2001, Bussler 2002, Mazzei et al. 2011, Kovács et al. 2012, Eckelt et al. 2014) and, therefore, a major part of the species' distribution range has not been considered in conservation plans. More studies and conservation efforts for *C. cinnaberinus* are thus needed in montane and traditional forest habitats. Focusing only on current population strongholds found in poplar lignicultures and even in invasive tree species stands in the lowlands might be a Trojan horse in *C. cinnaberinus* conservation efforts (Horák et al. 2010). The development of more efficient detection methods based on species pheromones or other semiochemicals that attract species would be helpful in further conservation studies (Larsson 2016), especially in sub-optimal but widespread species habitats.

In this study, low as well as high elevation habitats were included and, in both habitats, the amount of deadwood, amount of deciduous trees and degree of canopy openness was positively associated with *C. cinnaberinus* probability of occurrence, a fact which was in agreement with other studies on species habitat preference (Horák et al. 2010, Horák et al. 2011). Altitude had a negative effect on species distribution, meaning that, in stands with the same amount of deadwood, the species would be less abundant at higher elevations. A possible explanation could simply be macrophysiological. In ectotherm species, a restricted optimal temperature window at higher altitudes in comparison with lower altitudes might play a decisive role in the species' overall metabolic performance which is reflected in its life-history traits, including its reproduction and development rate (Gaston et al. 2009). Although the development cycle is still not well studied in *C. cinnaberinus*, Palm (1951) reported that larval development should take at least two years. Nevertheless, the duration of larval development could differ greatly between different climates, as shown for example in the stag beetle *(Lucanus cervus)*, in which the duration of the larval stage can vary from 3 to 6 years and even the number of larval instars can differ regionally (Harvey et al. 2011). *C. cinnaberinus* is a widespread species, ranging from boreal to warm temperate climates (Horák and Chobot 2009) and also has a wide altitudinal distribution as shown in this study. Its metabolic performance and life history traits might however change with latitude and altitude. Overall, it seems that the species' optimal conditions are in middle European lowlands in a warm temperate climate with hot and humid summers (Kottek et al. 2006, Horák et al. 2010). In Slovenia, such conditions are found only in the eastern part of the country, while the rest of the country is mountainous, which might be the reason for the lower *C. cinnaberinus* abundance. A second explanation for the effect of altitude could however be ecological, i.e. differences in habitat quality in lowland vs. montane forests. In future studies, the effects of climate conditions on *C. cinnaberinus* distribution patterns should be further examined, especially the effects of temperature and precipitation, to reveal their direct impacts on species life cycles and possible indirect impacts due to habitat structure alterations.

The size of the deadwood has been shown in this and other studies to be important for saproxylic beetles which prefer longer tree trunks with a larger diameter (Jonsson et al. 2005, Lindhe et al. 2005, Jonsell et al. 2007, Jonsell 2008). Although *C. cinnaberinus* was found in a number of host tree species and tree species was not found to be an important predictor in species microhabitat selection in lowland forests (Horák et al. 2011), it was found that tree host species might be important in the overall microhabitat performance of *C. cinnaberinus*. In such opportunistic species, the availability of host tree species should play a crucial role in host selection, where the most abundant tree species in a particular forest stand is also the most frequently occupied. That was the case for *Salix* in our sample of inspected trees and for *Pinus* in Southern Italy (Mazzei et al. 2011).

On the other hand, preferred or optimal tree hosts that are selected in a larger proportion than that available, could facilitate species establishment, population growth or even spread. *Tilia, Populus* and *Robinia* in particular, as tree species, were significantly preferred by *C. cinnaberinus*. Various poplar species were frequently reported as host trees of *C. cinnaberinus* in lowlands as well as in higher elevation forests (Horák et al. 2010, Eckelt et al. 2014, Marczak 2016). In this study, in addition to poplars, invasive Black Locust was found to be the preferred tree host in lowland forest. In addition to *Robinia*, other alien tree species, such as *Aesculus* and *Ailanthus*, were also reported as host trees in Austria, although at low frequencies (Eckelt et al. 2014).

The significant shift from native to invasive tree hosts revealed in this study indicates the great adaptive potential of *C. cinnaberinus*, particularly for rapid growing and short-lived species which could produce larger quantities of deadwood mass over shorter periods. The increase in growing stock and consequently in the deadwood of preferred host tree species in lowland forest stands in Slovenia, especially of *Populus* and *Robinia*, started in the period from the 1960s onwards (Božič and Krajnc 2012, Kutnar and Kobler 2013) and probably created optimal habitat conditions for *C. cinnaberinus*, resulting in an increase in its population and its eventual spread (Horák et al. 2010).

In contrast, there are no such conditions in montane forests where trees such as *Fagus, Abies* and *Picea* predominate in the growing stock (Marinček 1987) but were not found amongst the preferred species in this study or in those of others (Eckelt et al. 2014, Marczak 2016). On the other hand, *Tilia*, which is a preferred host tree in montane forests, has a low growing stock (<1 %) in the montane forests of Slovenia (Puncer 1980) and, therefore, the abundance and population size of *C. cinnaberinus* is constrained in these stands. Montane *C. cinnaberinus* populations thus remain low and scattered despite the beetle also being found in other dominant tree species in these environments, including *Fagus*, *Abies* and *Picea* (Eckelt et al. 2014, this study).

Conclusions

In conclusion, this study presents new findings regarding the ecology of *C. cinnaberinus* at the limit of its distribution in two types of species habitat that greatly differ in species abundance and overall ecological performance: lowland and montane forests. The study revealed the importance of montane forests for *C. cinnaberinus* conservation, although recent population strongholds are located in lowland riparian forests and lignicultures, these being a consequence of human-induced changes in forest structure due to poplar plantings and expansion of fast growing alien tree species.

To evaluate the future potential of *C. cinnaberinus* expansion and to define conservation management of existing populations, it is necessary to explore the impact of environmental factors that limit the species' distribution, in particular climate (effects of environmental temperature and precipitation) and tree species structure in forest stands. Future environmental change scenarios (climate change, invasion of alien tree species) may cause *C. cinnaberinus* population decline in some regions as well as an increase and expansion in other regions of Europe due to the apparently high dispersal and colonisation capacity of the species (Horák et al. 2010).

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Appendix

Table S1. Overview of the number of published research papers considering at least one of the 21 saproxylic beetle species of European conservation concern and listed on the Web of Science up to the year 2017. Specifically, the number of papers targeting certain species and the number of papers dealing with ecological, monitoring and conservation aspects of the species is given.

Species	Total no. papers	Species targeted papers	Ecology, Monitoring, Conservation	Ecology, Monitoring, Conservation – species targeted
Osmoderma eremita	68	36	61	32
Morimus funereus	50	46	5	3
Lucanus cervus	32	21	19	13
Rosalia alpina	17	14	14	11
Cucujus cinnaberinus	13	7	10	5
Cerambyx cerdo	12	9	7	4
Limoniscus violaceus	9	3	9	3
Pytho kolwensis	5	1	3	1
Boros schneideri	4	3	4	3
Mesosa myops	4	3	2	1
Stephanopachys substriatus	2	0	2	0
Rhysodes sulcatus	2	0	1	0
Agathidium pulchellum	1	1	1	1
Buprestis splendens	1	0	1	0
Phryganophilus ruficollis	1	0	1	0
Stephanopachys linearis	1	0	1	0
Xyletinus tremulicola	1	1	1	1
Propomacrus cypriacus	1	0	0	0
Corticaria planula	0	0	0	0
Oxyporus mannerheimii	0	0	0	0
Pseudogaurotina excellens	0	0	0	0