



Habitat requirements of deadwood-dependent invertebrates that occupy tree hollows

Thomas Ranius^{1,*} , Philip Gibbons² and David Lindenmayer² 

¹*Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, Uppsala 750 07, Sweden*

²*Fenner School of Environment and Society, Australian National University, Frank Fenner Building 141, Linnaeus Way, Canberra, Australian Capital Territory 2601, Australia*

ABSTRACT

Tree hollows support a specialised species-rich fauna. We review the habitat requirements of saproxylic (= deadwood dependent) invertebrates which occupy tree hollows. We focus on studies quantifying relationships between species occurrence patterns and characteristics of tree hollows, hollow trees, and the surrounding landscape. We also explore the processes influencing species occurrence patterns by reviewing studies on the spatio-temporal dynamics of populations, including their dispersal and genetic structure. Our literature search in the database *Scopus* identified 52 relevant publications, all of which were studies from Europe. The dominant taxonomic group studied was beetles. Invertebrates in hollow trees were often more likely to be recorded in trees with characteristics reflecting a large amount of resources or a stable and warm microclimate, such as a large diameter, large amounts of wood mould (= loose material accumulated in the hollows mainly consisting of decaying wood), a high level of sun exposure, and with entrance holes that are large and either at a low or high height, and in dry hollows, with entrances not directed upwards. A stable microclimate is probably a key factor why some species of saproxylic invertebrates are confined to tree hollows. Other factors that are different in comparison to downed dead wood is the fact that hollows at a given height from the ground provide shelter from ground-living predators, that hollows persist for longer, and that the content of nutrients might be enhanced by the accumulation of dead leaves, insect frass, and remains from dead insects. Several studies have identified a positive relationship between species occupancy per tree and the amount of habitat in the surrounding landscape, with a variation in the spatial scale at which characteristics of the surrounding landscape had the strongest effect over spatial scales from 200 to 3000 m. We found empirical support for the extinction threshold hypothesis, which predicts that the frequency of species presence per tree is greater if a certain number of trees are aggregated into a few large clusters of hollow trees rather than distributed among many small clusters. Observed thresholds in species occurrence patterns can be explained by colonisation–extinction dynamics, with species occupancy per tree influenced by variation in rates of immigration. Consistent with this assumption, field studies suggest that dispersal rate and range can be low for invertebrates occupying tree hollows, although higher in a warmer climate. For one species in which population dynamics has been studied over 25 years (*Osmoderma eremita*), the observed population dynamics have characteristics of a “habitat-tracking metapopulation”, as local extinctions from trees occur possibly because those trees become unsuitable as well as due to stochastic processes in small populations. The persistence of invertebrate fauna confined to tree hollows may be improved by prolonging the standing life of existing hollow trees. It is also important to recruit new generations of hollow trees, preferably close to existing larger groups of hollow trees. Thus, the spatio-temporal dynamics of hollow trees is crucial for the invertebrate fauna that rely upon them.

Key words: ancient trees, beetles, cavity, conservation, dispersal, extinction threshold, metapopulation, microclimate, saproxylic.

CONTENTS

I. Introduction	2023
II. Methods	2025

* Author for correspondence (Tel.: +46 768 24 44 35; E-mail: thomas.ranius@slu.se).

III. Results	2026
(1) Occurrence patterns in relation to characteristics at hollow and tree level	2026
(2) Occurrence patterns in relation to characteristics of the surrounding landscapes	2028
(3) Population dynamics	2028
(4) Direct observations of dispersal between trees	2028
(5) Genetic structure	2028
IV. Discussion	2029
(1) Occurrence patterns in relation to characteristics at the hollow and tree level	2029
(a) Microclimate	2029
(b) Food resources	2029
(c) Hollow trees as shelter	2030
(d) Temporal longevity	2030
(2) Observed occurrence patterns in the context of metapopulation theory	2030
(3) Observed processes in the context of metapopulation theory	2031
(4) Dispersal and genetic structure	2031
(5) Knowledge gaps	2031
V. Conclusions	2032
VI. References	2032
VII. Supporting information	2034

I. INTRODUCTION

When trees age, microhabitats are formed that are rare in younger trees (Lindenmayer & Laurance, 2017). Tree hollows are one such microhabitat (Kozák *et al.*, 2023). We define tree hollows as cavities that connect decaying wood within the trunk or limbs of standing living or dead trees with the external environment. The inner parts of the hollows are wider than the entrance, and they are larger than the galleries formed by inhabiting invertebrates. Much ecological research has been conducted on vertebrate fauna inhabiting tree hollows, especially birds and mammals (e.g. Gibbons & Lindenmayer, 2002). However, tree hollows are also important for many invertebrate species (Micó, 2018).

Research on invertebrates using tree hollows has focused on three areas. First, considerable attention has been paid to the invertebrate fauna using water-filled hollows for reproduction (reviewed by Petermann & Gossner, 2022). Interest in this fauna has often been motivated by the fact that some species are potential vectors for diseases, such as malaria (e.g. Omlin *et al.*, 2007). Second, some studies have focused on invertebrates using both tree hollows and other types of shelter for nesting and overwintering. Among these investigations, the most frequently studied taxa are stingless bees that produce honey (e.g. Eltz *et al.*, 2003). Finally, tree hollows are a microhabitat for saproxylic (= deadwood dependent) invertebrates, which use hollows for all or part of their life cycle (Siitonen & Ranius, 2015). Research on this group has been motivated, in part, by a concern for their conservation (e.g. Nilsson & Baranowski, 1997).

This review focuses on the habitat requirements of saproxylic invertebrates observed in tree hollows. Saproxylic invertebrates include species dependent on fungal decay of wood, or upon the presence of other saproxylic organisms (i.e. including predators and parasites) both in living and dead trees (Alexander, 2008). As an example, it has been

estimated that in Fennoscandia around 50% of saproxylic beetles can use dead wood in large old trees. Of all saproxylic beetle species, 10% are dependent on tree hollows, whereas a lower number of species is dependent on other microhabitats in large old trees (Ranius *et al.*, 2024). For hollow-dwelling saproxylic invertebrates, larval development takes place in a hollow (Palm, 1959). Some species spend their entire life cycle in tree hollows (Hedin *et al.*, 2008), whereas others visit other microhabitats to find food, such as flowers (Wetherbee *et al.*, 2020a). To the best of our knowledge, a synthesis of current knowledge about hollow-dwelling saproxylic invertebrates is lacking [but see Micó (2018) for an overview of the invertebrate fauna in tree hollows].

Many populations of invertebrates that use tree hollows are assumed to be declining (Cálix *et al.*, 2018). This assumption is based primarily on knowledge about the generally negative trends documented for populations of old large-diameter trees with hollows (Lindenmayer, Laurance & Franklin, 2012). Several factors are leading to tree hollows becoming scarce. First, forestry has a strong negative effect, since hollows occur almost only in trees older than the typical rotation time in wood-production forestry (e.g. Gibbons, McElhinny & Lindenmayer, 2010; Ranius, Niklasson & Berg, 2009a). Furthermore, in Europe, Asia and Australia, ancient trees persist in traditional agricultural landscapes (Manning, Fischer & Lindenmayer, 2006; Hartel *et al.*, 2013; Kadej *et al.*, 2016). Such trees are threatened both by abandonment of agricultural land (generating overshading, which may shorten the life of existing trees and decrease recruitment) and intensification of agricultural management which involves clearing remnant trees or inhibits regeneration (Gibbons *et al.*, 2008; Hartel *et al.*, 2013; Nolan *et al.*, 2020). In urban areas, hollow trees are under threat because of public safety concerns (Carpaneto *et al.*, 2010), a lack of adequate recruitment (Le Roux *et al.*, 2014), and the land they occupy being in demand for housing

(Parsons *et al.*, 2023). Other factors reducing the abundance of tree hollows include climate warming, and an associated increased frequency of stormfelling and forest fires (Woolley *et al.*, 2018), and dieback due to tree diseases (Pautasso *et al.*, 2013).

Conservation of invertebrates in tree hollows can be motivated not only by the value of biodiversity itself, but also because invertebrates in tree hollows have several key ecological functions. First, at least some species are important decomposers in tree hollows (Mestre, Jansson & Ranius, 2018; Wetherbee *et al.*, 2022), reducing the size of dead wood fragments and increasing N and P concentrations (Jönsson, Méndez & Ranius, 2004; Sánchez *et al.*, 2017; Wetherbee *et al.*, 2022), although this does not imply they affect dead wood decomposition rates in the surroundings of hollow trees (Wetherbee *et al.*, 2021). Since invertebrates speed up the decomposition of dead wood in hollows, they probably also contribute to the formation and expansion of tree hollows (Gibbons & Lindenmayer, 2002). For that reason, it has been suggested that invertebrates involved in the decomposition of wood in tree hollows are ecosystem engineers (Sánchez-Galván *et al.*, 2014). Second, invertebrates may influence ecosystems in nearby areas, such as acting as natural enemies in pest control (Wetherbee, Birkemoe & Sverdrup-Thygeson, 2020b). Invertebrates in tree hollows can also improve conditions for other species. For instance, the nests of ants may improve thermal conditions for nesting birds (Mitrus, Hebda & Wesłowski, 2016).

Hollow-bearing trees are often long-lived. In pedunculate oak (*Quercus robur*), in which much of the research on invertebrates occupying hollow trees has been conducted, hollows start to form when the trees are at least 200 years old (Ranius *et al.*, 2009a). These hollow trees can persist for another one or more centuries (Ranius *et al.*, 2009b). In pedunculate oak, most hollows are formed around scars remaining after large branches have shed. However, the typical process of tree hollow formation can vary among tree species and biogeographic realms. For instance, in Northern America woodpeckers are important (Cockle, Martin & Wesłowski, 2011), whereas in Australia the activities of termites and fungi are more important factors contributing to hollow formation (Gibbons & Lindenmayer, 2002).

The probability that a species is threatened is related, in part, to species traits (Hagge *et al.*, 2021). It has been suggested that invertebrates occupying tree hollows have a low dispersal ability as an adaptation to a stable habitat (Nilsson & Baranowski, 1997; Percel, Laroche & Bouget, 2019). This is because hollow-bearing trees are often long-lived and there may be high densities of hollow trees in many unmanaged stands (Nilsson *et al.*, 2006; McLean *et al.*, 2015). This can make inhabiting fauna sensitive to habitat fragmentation (Ranius, 2002), which can be assessed from the shape of relationships between species occupancy and habitat amount. Fahrig (2003) formulated two competing hypotheses to explain species occurrence in fragmented landscapes: the proportional area hypothesis and the

extinction threshold hypothesis. Which of these holds has consequences for conservation strategies. The proportional area hypothesis implies that the total population size of a species per unit area of habitat is constant and independent of whether the total area of habitat is divided into a few larger fragments or many smaller fragments. Conversely, the extinction threshold hypothesis predicts that many small fragments support a smaller total population than one large fragment of the same total area. This means there is a negative effect of many small fragments, especially if those fragments are below certain threshold sizes. These hypotheses can be tested by sampling the abundance of species in habitat fragments of varying size.

Here we review factors associated with the occurrence of invertebrates in tree hollows. These factors include the characteristics of hollows, trees, and the surrounding landscape, and ecological processes (including population dynamics and dispersal) that potentially influence observed patterns of occurrence. We focus on these aspects because they are important when prioritising decisions for nature conservation. Knowledge about occurrence patterns is important for understanding which trees and which locations are most valuable to conserve in the short term, while knowledge about underlying ecological processes is important when developing strategies for the conservation of invertebrate fauna in the long term. Thus all aspects reflect the requirements of this fauna, in the short and long term, respectively. More specifically, we searched for studies giving answers to the following questions: (i) which characteristics of hollow trees and hollows are correlated with the occurrence of invertebrates? (ii) What is the effect of the spatial location of hollow trees in relation to other hollow trees on per-tree occurrence patterns? (iii) Which characteristics of the surrounding landscapes are correlated with per-tree occurrence patterns? (iv) What characterises the colonisation–extinction dynamics of invertebrates in hollow trees, and is there any empirical support for various types of metapopulation dynamics (as described by e.g. Harrison & Taylor, 1997)? (v) What is the dispersal rate and range of saproxylic invertebrates in hollow trees? (vi) Does the pattern of genetic differentiation among populations suggest dispersal limitation?

At individual hollow and tree scales, our main hypothesis was that species occurrence patterns of invertebrates would be affected by characteristics of the trees and hollows reflecting their microclimate, food resources, value as shelter, and longevity. Furthermore, we hypothesised that other woody microhabitats would differ in these characteristics, and that this may explain why particular species are confined to tree hollows. At a landscape scale, we hypothesised that some species have extinction thresholds generated by metapopulation dynamics (Lande, 1987), which makes the dispersal rates and patterns of local extinctions in trees important for understanding colonisation–extinction dynamics occurrence patterns in landscapes. We searched for empirical studies of these patterns and processes by analysing the global scientific literature.

II. METHODS

Our intention was to perform a comprehensive search of the literature that addressed one or more of our six key questions about the ecology of saproxylic invertebrates inhabiting tree hollows (Table 1). Since it proved to be impossible to create search strings specifically focusing on these questions without missing relevant studies, as a first step, we searched for all literature on invertebrates inhabiting tree hollows in the *Scopus* database. We used the following search string to identify studies that included at least one term related to tree hollows and one term related to invertebrates. We included the taxa listed in the string below as all are known to use tree hollows (Siitonen & Ranius, 2015).

TITLE-ABS-KEY (tree AND hole OR hollow OR cavity AND invertebrate OR arthropod OR insect OR beetle OR gnat OR fly OR ant OR wasp OR ant OR springtail OR mite OR spider OR harvestman OR pseudoscorpion OR woodlice OR centipede OR millipede OR Coleoptera OR Diptera OR Hymenoptera OR Collembola OR Acari OR Araneae OR Opiliones OR Pseudoscorpionida OR Isopoda OR Chilopoda OR Diplopoda).

From our search, we obtained 1623 publications. During a first screening of titles and abstracts, we removed papers that were: (i) not about tree hollows, or (ii) only about taxa other than saproxylic invertebrates, or (iii) were concerned only with systematics or natural history (e.g. descriptions of new species or records of species in a specific area). This initial screening reduced our corpus to 183 publications. During a second screening, we read each paper in its entirety and retained those that gathered empirical data in a standardised way to answer our six questions (Table 1). We specifically checked that the approach to standardise the sampling for all included trees was described and appropriate. Relevant studies were those that had been conducted in tree hollows, in boxes emulating tree hollows (Jansson *et al.*, 2009), or on species described as associated with tree hollows conducted in any environment (including e.g. laboratory experiments). More specific eligibility criteria for each question are given in Table 1. The retained studies were all published in peer-reviewed scientific journals. The initial search was undertaken on November 17 2022. One author (T.R.) was responsible for the literature search.

Based on the retained studies, we completed a narrative assessment. For four of our questions (iii–vi), we found only

Table 1. Questions for which we searched for answers in the scientific literature and question-specific eligibility criteria used. All questions are regarding saproxylic invertebrates in tree hollows. Some of the papers answered more than one question, and the results were then counted for more than one question.

Question	Eligibility criteria	Number of studies
Which characteristics of hollow trees are correlated with the occurrence of invertebrates?	The response variable should include species richness (or other diversity metrics) or frequency of occurrence of species, but not only species composition. Characteristics of the trees include the immediate surroundings of the trees. Correlations between saproxylic invertebrates and characteristics such as chemical characteristics or occurrence of other invertebrate species are not included, since correlations can arise because saproxylic invertebrate fauna can affect these characteristics.	27
What is the effect of the spatial location of hollow trees in relation to other hollow trees on per-tree occurrence patterns?	Spatial location is reflected in variables such as distance to nearest neighbour, amount of potential dispersal sources within sites or buffers, or variables weighted in relation to distance, such as connectivity metrics used in metapopulation ecology.	18
Which characteristics of the surrounding landscapes are correlated with per-tree occurrence patterns?	This includes characteristics at scales larger than the immediate surroundings of the trees, possibly both quantitative buffer metrics as well as more qualitative categorisation.	6
What characterises the colonisation–extinction dynamics of invertebrates in hollow trees, and is there any empirical support for various types of metapopulation dynamics (as described by e.g. Harrison & Taylor, 1997)?	This includes field observations repeated so that colonisations and local extinctions could potentially be observed or results from simulations of population development over time based on field data.	4
What is the dispersal rate and range of saproxylic invertebrates in hollow trees?	All direct observations of dispersals are included. Estimates of dispersal rates and ranges require more than single observations.	8
Does the pattern of genetic differentiation among populations suggest dispersal limitation?	Studies reporting genetic structure at any spatial scale are included.	4
Total		52

a few studies for each question, and their contributions to the answers were not all of the same type, which meant that a quantitative compilation of findings was not possible. Given this, we compiled the results as narrative summaries. By contrast, there was a larger set of studies for questions *i* and *ii*, many of which employed a rather similar approach. For those studies with a similar response variable, such as species richness of saproxylic beetles, we initially considered conducting a meta-analysis. However, almost no studies provided effect sizes for non-significant tested variables nor information on standard errors of effect sizes. Therefore, we present data on how many studies tested each variable, and which proportion of these identified the variable as significant ($P < 0.05$, or with the akaike information criterion (AIC) value decreasing when including the variable), and whether a positive or negative relationship was identified. Since studies of species richness contain more information than studies of certain groups of species or individual species, we present data from these two kinds of studies separately.

III. RESULTS

We identified 52 papers that addressed at least one of our questions (Table 1; see online Supporting Information, Appendix S1). All were empirical field studies from Europe. Beetles were by far the most studied group, but we also found four papers on pseudoscorpions, two on flies, and one on spiders. Of these 52 papers, 33 focused on one or a few invertebrate species confined to tree hollows, whereas 19 examined species richness, in most cases including all saproxylic beetle species, that is both species confined to tree hollows and those that also may occur in other types of dead wood. A majority of studies was conducted only in oak trees (*Quercus* spp.; 61%; Fig. 1A) or in several tree species (always including *Quercus* spp.) (27%). A small proportion (12%) focused on *Fagus* spp. or other tree species.

(1) Occurrence patterns in relation to characteristics at hollow and tree level

We found 26 field studies on relationships between characteristics of trees and tree hollows and the species richness or the presence/absence of saproxylic invertebrates (Appendix S1). Only one laboratory study examined the willingness of females to lay eggs in substrates that were the contents of tree hollows (Landvik, Niemelä & Roslin, 2016a). Thus, current knowledge mostly documents occurrence patterns rather than mechanisms in the life cycle that underpin these occurrence patterns. The study on egg-laying behaviour revealed that the fastest larval growth and highest survival rate occurred in the types of substrate where females preferred to lay their eggs (Landvik *et al.*, 2016a). Therefore, the occurrence patterns observed in the field probably reflect both the preferences of individuals and their survival rates.

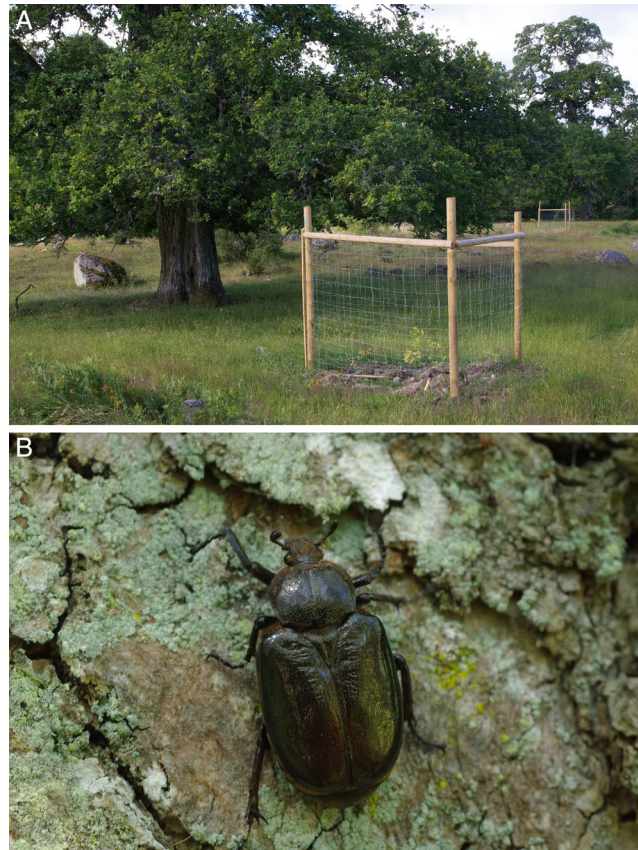


Fig. 1. (A) Studies on saproxylic invertebrates in hollow trees have, to a large extent, been conducted in pedunculate oak *Quercus robur*. Locations with a high density of hollow oaks in Northern Europe often have a long history of management for hay-making and grazing. If grazing pressure is intense, small enclosures are sometimes constructed to allow oak regeneration. Photograph: Thomas Ranius. (B) Ecological studies on invertebrates in hollow trees often use *Osmoderma eremita* (or *O. barnabita*) as a model species. It is a 3-cm-long scarabaeid beetle. Photograph: Thomas Ranius.

In the field studies, there was high variation in how often different characteristics were analysed (Table 2). Tree diameter was often tested, and usually had a positive effect. Other factors that were frequently tested were canopy cover (including measures reflecting regrowth of younger trees) and moisture level (including accumulated water and upward entrance orientation), both of which had negative effects, whereas the amount of wood mould (but not the volume of the hollow) had a positive effect. The size of the entrance hole and the height of the entrance hole in relation to the ground, also were important variables, although effects varied from positive to negative depending on the species and study (Table 2).

The effect of tree species has been tested in five studies. Some saproxylic invertebrates in hollow trees occur more frequently in certain tree species, such as linden *Tilia chordata* and pedunculate oak (Table 2). In a comparison of four

Table 2. Summary of results presented in the scientific literature about the relationship between tree and tree hollow characteristics and invertebrates.

Tree and hollow characteristics	Species richness		Certain groups		Species		Total
	Tested	Result	Tested	Result	Tested	Result	Tested
Diameter	7	3 pos	21	3 pos	18	11 pos	46
Height	5	1 pos, 2 neg	18	4 neg	17	7 pos, 2 neg	40
Size of entrance	5	2 pos, 1 int	18	4 pos	7	1 pos	30
Entrance oriented to S or SW	2	0	15	0	8	1 pos	25
Canopy cover	5	1 neg	0	0	14	3 neg	19
Volume of the hollow	3	0	15	3	0	0	18
Amount of wood mould	2	1 pos	0	0	15	7 pos	17
Vertebrate remains	0	0	15	0	2	0	17
Entrance upwards	2	1 neg	0	0	13	4 neg	15
Water accumulated	0	0	15	3 neg	0	0	15
Tree species	1	1 (oak)	0	0	4	2 (oak, linden, alder)	5
Type of rot (brown/white)	1	0	0	0	4	0	5
Foliage density	0	0	0	0	5	0	5
Forest regrowth	1	1 neg	3	1 pos, 2 neg	0	0	4
Wood mould moisture	1	0	0	0	3	1 neg	4
Distance to wood mould surface	1	0	0	0	3	1 pos	4
Living/dead	0	0	0	0	4	1 pos	4
Stage of decomposition	2	2 neg	0	0	1	1 pos	3
Tree vitality	1	0	0	0	2	0	3
Original canopy cover	2	2 neg	0	0	0	0	2
Proportion wood mould per unit soil	1	0	0	0	1	1 pos	2
Height above sea level	1	1 neg	0	0	0	0	1
Dead branches	1	0	0	0	0	0	1
Tree growth rate	0	0	0	0	1	1 neg	1
Tree age	0	0	0	0	1	1 pos	1

“Species richness” includes studies with a response variable reflecting species richness of an invertebrate group (in most cases saproxylic beetles), “Certain groups” includes studies reporting species richness of certain selected ecological groups, and “Species” includes studies with a response variable reflecting frequency of occurrence (or abundance) of certain species. “Tested” is the number of tests we included for this variable, and “Result” is the number of tests where the outcome was statistically significant [$P < 0.05$ or decreasing AIC (Akaike Information Criterion) value with inclusion of the variable]. See Appendix S2 for details of the tests.

different tree species in Northern Europe, most beetle species used several tree species, although most occurred more frequently in pedunculate oak (Milberg *et al.*, 2014).

Three studies related occurrence patterns of saproxylic beetles to microclimatic variables, although with varying outcomes. Schauer *et al.* (2018b) found that total species richness increased with mean temperature during the sampling period, while, unexpectedly, the opposite result was found for species on the German Red List. *Osmoderma eremita* occurred more frequently in hollows with a warmer and more stable microclimate (Lindman, Öckinger & Ranius, 2023). Henneberg *et al.* (2021) found overall no relationship between temperatures inside tree hollows and species richness of saproxylic beetles, but in one study region the relationship was hump-shaped, that is the highest species richness was in tree hollows with an intermediate temperature.

(2) Occurrence patterns in relation to characteristics of the surrounding landscapes

We found 18 studies on relationships between species' per-tree occurrence patterns and the spatial location of hollow

trees in the landscape. Note that five of these investigations were not independent, since they partly used the same data sets (see Appendix S1). In six independent investigations, some tests showed a positive relationship between species occupancy or species richness per tree and the number of hollow trees in surrounding area (Musa *et al.*, 2013; Pilskog *et al.*, 2018; Ranius, Johansson & Fahrig, 2011) or a negative effect of the distance to potential dispersal sources (Jansson *et al.*, 2009; Kadej *et al.*, 2016; Mestre *et al.*, 2018). These studies all tested tree abundances or distances over a larger scale (with a radius of 1 km or more), or had an experimental design that sampled extremes in habitat isolation. By contrast, six observational studies conducted at a small scale (up to 500 m) showed no effect of isolation (Ranius & Nilsson, 1997; Carpaneto *et al.*, 2010; Chiari *et al.*, 2012; Goux *et al.*, 2015; Pilskog *et al.*, 2016; Schauer *et al.*, 2018b). One study contained evidence that for beetles in tree hollows, the spatial scale at which characteristics of the surrounding landscape had the strongest effect was smaller in comparison to beetles in more short-lived deadwood habitats (Percel *et al.*, 2019). However, among beetle species using tree hollows, the spatial scale at which tree abundances of the surrounding landscape had the strongest effect on

species occurrences varied widely, with radii from about 200 to 3000 m (Ranius *et al.*, 2011).

We identified two studies that compared sites with a large *versus* small number of hollow trees. The results of both investigations supported the extinction threshold hypothesis; they contained evidence of lower species richness or lower frequency of occurrence per tree in smaller tree clusters (Nilsson & Baranowski, 1997; Ranius, 2002). No studies supported the proportional area hypothesis.

Five studies assessed the effect of other aspects of the surrounding landscape than the abundance of hollow trees. Two compared hollow trees in forests with those in agricultural landscapes, and found large differences in species composition (Sverdrup-Thygeson, Skarpaas & Ødegaard, 2010; Parmain & Bouget, 2018). This can be partly explained by differences in habitat openness, since canopy cover can be important in studies at a tree level (Table 2). However, other tree characteristics, such as diameter, number of microhabitats present, and tree morphology, also differ between trees in these environments (Sverdrup-Thygeson *et al.*, 2010; Parmain & Bouget, 2018), and may affect the beetle fauna in and around hollow trees.

The effect of resources in the surroundings of hollow trees has rarely been studied; we found only four papers that included such attributes. For instance, many beetles characterised by a larval development stage in hollow trees visit flowers (Wetherbee *et al.*, 2020a). However, we found no studies examining whether the abundance of flowers in the surrounding area can be a factor limiting beetles that occupy hollow trees. Sverdrup-Thygeson *et al.* (2010) identified a positive effect of dead wood in the surrounding landscape on the number of red-listed saproxylic beetles captured per trap placed in hollow trees. However, since they used flight-interception traps, which collect beetles occupying tree hollows as well as other habitats, this study does not show that beetles occupying tree hollows are affected by other types of dead wood in the surrounding landscape. Studies using emergence traps, which sample only beetles from tree hollows, have obtained mixed outcomes for the effect of dead wood and deadwood-related tree microhabitats on beetles in tree hollows; the relationship has been found to be positive or neutral (Henneberg *et al.*, 2021), or negative (Schauer *et al.*, 2018b).

In a comparison of hollow trees in parks (where dead wood occurred only in the tree hollows of linden) and wooded meadows (where dead wood also can occur as downed and standing dead wood and of other tree species), there was very limited difference in the number of beetle species associated with tree hollows, although the total number of saproxylic beetle species was higher in wooded meadows (Jonsell, 2012). Thus, there was only limited evidence in the literature about whether resources outside hollow trees are important for the fauna in tree hollows.

(3) Population dynamics

Four studies examined temporal dynamics of invertebrate populations occupying tree hollows. All used time series of

population assessments and three related population dynamics to habitat dynamics.

Based on time series data, population dynamics have been studied in two saproxylic beetle species occupying tree hollows: *Tenebrio opacus* has been studied over 6 years (Laroche, Paltto & Ranius, 2018), and *O. eremita* over 25 years (Lindman *et al.*, 2020; data from the first five and seven years, respectively, also used by Ranius, 2001, 2007; Fig. 1B). Both investigations identified wide variation in beetle population size among hollow trees. Over a 25-year period, the total population size of *O. eremita* changed little, but in most trees with the species present, there was a clear positive or negative trend in population size over time, implying that trees hosting the largest populations in the later years were different from those in the early years of the investigation.

(4) Direct observations of dispersal between trees

We found eight studies that examined the dispersal of beetles between hollow trees using direct observations, with six investigations based on more than a single observed dispersal event. All investigations focused on *O. eremita*. Capture–recapture and radiotracking work in Sweden suggested a dispersal rate (proportion of individuals leaving their natal tree for another hollow tree) of 15% and an average dispersal distance of approximately 60 m (Ranius & Hedin, 2001; Hedin *et al.*, 2008). However, using a different method, Larsson & Svensson (2009) observed a dispersal rate of at least 50% for the same species in the same study area. Svensson *et al.* (2011) observed a mean dispersal range of around 80 m and did not observe any difference in the outcomes using different methods. Chari *et al.* (2013), who studied *O. eremita* in Italy, observed dispersal rates of 60–70%. A comparison of flight activity of *O. eremita* both within and among years, showed that it was positively influenced by temperature (Larsson & Svensson, 2011).

(5) Genetic structure

We found four studies on genetic structure that considered eight species (five beetles, two pseudoscorpions, and one fly species) associated with hollow trees. For three of these species, earlier studies of their spatial occurrence patterns (or for *Osmoderma barnabita* those of a closely related species, *O. eremita*; Ranius *et al.*, 2011) indicated dispersal limitation, with a higher frequency of occurrence per tree in trees with a higher level of connectivity to other hollow trees (*Elater ferrugineus* and *Larca lata*; Ranius *et al.*, 2011). By contrast, for two of the studied species, no positive effect of connectivity was found (*Protaetia marmorata* and *Allochernes wideri*; Ranius *et al.*, 2011), while the remaining three species have not been studied in this regard (*Anaspis ruficollis*, *Criorhina floccosa*, and *Xylomya maculata*). For the first three species, genetic structure was qualitatively consistent with spatial occurrence patterns: genetic distance was positively correlated with geographic distance, suggesting dispersal limitations for *Elater ferrugineus* (Oleksa *et al.*, 2015), *Larca lata* (Ranius & Douwes, 2002),

and *O. barnabita* (Oleksa *et al.*, 2013). By contrast, for species where connectivity had been studied, but no positive effects were observed, genetic distance was small and not correlated with geographic distance [*Allochemes wideri* (Ranius & Douwes, 2002); *Protaetia marmorata* (Oleksa *et al.*, 2013)]. Moreover, no indication of restricted gene flow was observed for those species for which no studies of spatial occurrence patterns have been conducted (Schauer *et al.*, 2018a). Genetic structure reflects not only ongoing dispersal, but also historical dispersal (Ranius & Douwes, 2002). In the studied landscapes, the historical amount of habitat has been either higher than today (Ranius & Douwes, 2002) or is not known, meaning that observed genetic structure might not reflect current conditions.

IV. DISCUSSION

(1) Occurrence patterns in relation to characteristics at the hollow and tree level

Our understanding of the importance of characteristics of trees and hollows for inhabiting invertebrate fauna is based primarily on snapshot observations of occurrence patterns. Little is known about the behaviour of individuals and population processes underpinning the observed patterns. There is one study on how occurrence patterns change over time (Lindman *et al.*, 2020) and one on how egg-laying behaviour and larval survival is affected by substrate contents (Landvik *et al.*, 2016a). The only aspect of behaviour among hollow-dwelling saproxylic invertebrates that has been researched in more than one study is the effect of pheromones emitted by beetles. Pheromones can attract conspecifics (Larsson *et al.*, 2003) but also specialised predators (Svensson, Larsson & Hedin, 2004).

Many invertebrate species found in tree hollows occur in other types of dead wood, but a large proportion is associated primarily with tree hollows (Milberg *et al.*, 2016; Ranius & Jansson, 2000). The large number of species associated with tree hollows may be a function of several factors, which also may affect their occurrence patterns. These factors include: (a) microclimate, (b) food resources, (c) provision of shelter, and (d) temporal longevity.

(a) Microclimate

The microclimate in tree hollows is more stable in comparison to downed wood or standing dead wood. In studies in south-eastern Sweden, daily temperature fluctuations were around 1 °C in tree hollows in oak pastures, 8 °C in standing and downed dead wood, and 11 °C in the air (Lindman, Öckinger & Ranius, 2022; Lindman *et al.*, 2023). The fact that tree hollows buffer climate fluctuations adds to findings at larger scales that old-growth forest structure can buffer populations from climate warming (Betts *et al.*, 2018). Thus, microclimatic conditions could be a key factor explaining

why many saproxylic invertebrate species are confined to tree hollows.

Microclimatic conditions may influence relationships between easily measured characteristics of trees and hollows and saproxylic fauna. Characteristics of trees and hollows that have been found to affect the occurrence of invertebrates are correlated with microclimatic temperature and moisture (Lindman *et al.*, 2023). Hollows in trees with large diameters have higher autumn and winter temperatures and lower summer temperature and temperature fluctuations than those in trees with small diameters. More open conditions tend to increase the temperature, especially in spring and autumn, with larger entrance holes leading to increased temperatures. Higher entrance height gives rise to drier conditions and also influences temperature, especially for warmer spring and summer temperatures. Hollows with a larger amount of wood mould volume are cooler. Finally, when the entrance is directed in an upward direction, moisture levels are higher and autumn temperature fluctuations lower (Lindman *et al.*, 2023). This strongly suggests that microclimatic conditions are important explanatory variables behind observed occurrence patterns in relation to characteristics of trees and hollows.

(b) Food resources

Many beetle species associated with tree hollows seem to develop and survive in a mixture of dead leaves and fresh sawdust (Mestre *et al.*, 2018). Furthermore, at least one beetle species (*O. barnabita*) that is confined to tree hollows, grows rapidly when fed only on dead leaves (Landvik *et al.*, 2016a). The use of dead leaves as a food may be one explanation why many saproxylic beetle species favour tree hollows, as dead leaves accumulate in tree hollows to a greater extent than in other types of dead wood. Nevertheless, since dead leaves represent a suitable diet for tree hollow specialists, there must be other factors, such as microclimate, that prevent them from breeding in other forms of compost. Most species in tree hollows can use several different tree species (Milberg *et al.*, 2014), suggesting they may be relatively insensitive to the chemistry of the wood. Thus, at least for these species, it is not specialisation on certain food resources that confines them to tree hollows.

Entomologists have identified beetle species associated with animal nests in hollows (Ranius & Jansson, 2000), perhaps reflecting the fact that animal nests add nutrients to the hollows. Furthermore, anecdotal observations exist of invertebrates inhabiting tree hollows that occur in association with nests and other animal remains outside tree hollows (Ranius & Wilander, 2000). However, the presence of remains from nests have not been found to increase the frequency of occurrence of saproxylic invertebrates [Table 2; note however that Quinto *et al.* (2014) observed some positive relationships with insect abundance].

Nevertheless, the availability of resources may be an important factor explaining invertebrate occurrence patterns in tree hollows. Positive effects on species occurrences of tree

diameter and amount of wood mould have been found (Table 2). Trees with a larger diameter and larger amounts of wood mould provide more extensive resources for saproxylic fauna, thereby hosting larger populations with smaller extinction risk (Ranius, 2007). Furthermore, larger diameter trees have more space to support a wider range of microhabitats for a larger number of species. However, tree diameter also affects microclimatic conditions (Lindman *et al.*, 2023) and reflects tree age (Ranius *et al.*, 2009b), which also might be important for invertebrate fauna.

Variation in the availability of food resources also may explain other relationships between species occurrence patterns and easily measured tree characteristics. A greater amount of dead leaves in tree hollows increases the availability of nutrients (Landvik *et al.*, 2016a); dead leaves are more abundant in tree hollows with larger entrance holes (Walker & Merritt, 1988) and this may explain the increased abundance of saproxylic beetles in such cavities (Table 2). Another reason why larger entrance holes indicate more resources is that there can be a positive correlation between the size of the entrance hole and wood mould volume and tree age (Ranius *et al.*, 2009b). Landvik *et al.* (2016a) found that frass from beetles has a much higher N content, as well as other important elements, than brown rotten wood. Since frass is more prevalent in later decay stages than brown rotten wood, this may explain why studies have shown higher frequency of occurrence in older trees and tree hollows in later stages (Table 2).

(c) *Hollow trees as shelter*

Tree hollows might provide shelter for invertebrates, potentially decreasing predation or parasitism risk. Hernández-Corral *et al.* (2021) found a lower abundance of invertebrate predators (spiders) in cavities that occur higher in the tree, suggesting that cavities above the ground provide some shelter from ground-living predators. However, we found no studies on the potential influence of predators on the saproxylic beetle fauna in tree hollows. Since a higher abundance and species richness of predators often leads to lower richness and biomass of prey (Katano *et al.*, 2015), an increased occurrence of saproxylic beetles in tree hollows at greater heights above the ground may reflect lower predation rates. However, for several species the opposite pattern was found, with a higher frequency of occurrence in cavities closer to the ground (Table 2).

(d) *Temporal longevity*

Tree hollows are a relatively long-lasting habitat compared with other types of dead wood. We hypothesised that it might take time for invertebrate fauna to colonise and occupy hollow trees due to limited dispersal ability, as has been found for epiphytes (Johansson, Ranius & Snäll, 2012). However, we found no support for time effects in the literature. For instance, a 25-year study of *O. eremita* revealed that populations fluctuated over time and that both colonisations and

local extinctions occurred, suggesting that slow accumulation of species is not the determining process. A 10-year study of boxes containing an artificial decaying wood habitat showed that there was no accumulation of species over time (Carlsson *et al.*, 2016).

(2) **Observed occurrence patterns in the context of metapopulation theory**

The extent to which metapopulation theory is relevant when predicting colonisation–extinction dynamics and occurrence patterns varies widely among study systems (Harrison & Taylor, 1997). Metapopulation dynamics is primarily applied to species confined to habitat patches surrounded by a matrix of non-habitat (Thomas, Thomas & Warren, 1992). In metapopulations, there is some dispersal between patches, which allows colonisation, but since dispersal is limited, a reduction in available habitat in the surrounding landscape decreases the probability of colonisation and increases the probability of extinction to the extent that species occupancy per habitat patch is decreased. The extent to which these criteria are fulfilled is dependent on both the biology of the species and characteristics of landscapes and habitat patches.

We found several studies showing an effect of the abundance of hollow trees in the surrounding landscape on per-tree occurrence of invertebrates in tree hollows. By contrast, there was no indication that any other features of the surrounding landscape were important. This suggests, consistent with metapopulation theory, that individual hollow trees constitute habitat patches, while the surrounding landscape may act as a non-habitat matrix.

We found two studies that provided empirical evidence for the extinction threshold hypothesis (Nilsson & Baranowski, 1997; Ranius, 2002). There is evidence for stronger dispersal limitation in cooler climates (Chiari *et al.*, 2013), but tests of the extinction threshold hypothesis have been conducted only in Sweden, close to the northern distribution limit of the species examined. Studies are lacking from other regions with a warmer climate, and thus it is unknown how general these patterns are.

Metapopulation theory provides a theoretical explanation for the existence of extinction thresholds (Lande, 1987), and the observed threshold patterns (Nilsson & Baranowski, 1997; Ranius, 2002) are consistent with metapopulation theory. They are also consistent with predictions of long-term population viability based on population size time series for one beetle species (Ranius, 2007). These observed threshold patterns have implications for conservation. In terms of per-tree occupancy of invertebrate species, large continuous areas are better than more fragmented hollow tree habitat. By contrast, widely spaced hollow-bearing trees remain suitable as habitat for mobile species such as birds (Le Roux *et al.*, 2018). An argument for protecting many small areas rather than a few large ones is that landscape-scale species richness can be higher in the former due to higher habitat heterogeneity and greater variability in species composition (Fahrig *et al.*, 2021). However, landscape-scale

species richness has not been assessed in any study of invertebrates in tree hollows.

(3) Observed processes in the context of metapopulation theory

Population dynamics, including colonisation–extinction dynamics, has been studied most extensively for *O. eremita* than for any other hollow-dependent invertebrate species (Fig. 1B). Given the wide variation in population sizes of hollow-dependent invertebrates among trees, it has been suggested that *O. eremita* has features of a “mainland–island metapopulation” (Ranius, 2007; *sensu* Harrison & Taylor, 1997), with much higher local extinction risk in trees that are “islands” in comparison to those that are “mainlands”. This pattern was also proposed for populations of *Tenebrio opacus* (Laroche *et al.*, 2018). However, since population sizes for both species can change rapidly over time (Laroche *et al.*, 2018; Lindman *et al.*, 2020), it is impossible to identify trees that act as a “mainland” in the long term, since all local populations are at risk of extinction over timescales of a few decades. Thus, these populations may function as mainland–island metapopulations over timescales of only a few years.

It has also been argued that *O. eremita* has features of a “habitat-tracking metapopulation” (Ranius, 2007). Habitat-tracking metapopulations are those that track the dynamics of their habitats, going extinct where habitat patches become unsuitable, and colonising both old and recently formed patches (Harrison & Taylor, 1997). Thus, they differ from “classic” metapopulations, in which local extinctions take place stochastically in small populations inhabiting habitat patches that later can be recolonised. A 25-year study of *O. eremita* revealed that extinctions from trees are partly due to habitat dynamics (i.e. trees collapse, making them unsuitable habitat), while others can be explained by stochastic processes in small populations (Lindman *et al.*, 2020). For *O. eremita*, colonisation rate increased with connectivity and tree characteristics reflecting early successional stages, while extinction rate increased with tree diameter, with a greater diameter found in trees at later stages (Lindman *et al.*, 2020). A space-for-time study showed that the largest populations of *O. eremita* were in trees 300–400 years old (Ranius *et al.*, 2009b). Hollow trees younger than 300 years often had limited wood mould, while trees older than 400 years were suitable but rare due to management history or natural tree mortality. Thus, the dynamics of hollow trees is important for the dynamics and persistence of these metapopulations.

(4) Dispersal and genetic structure

The dispersal of *O. eremita* has been assessed in several studies, but with contrasting results (Fig. 1B). One possible explanation for the relatively high dispersal rates observed by Larsson & Svensson (2009) in comparison to Ranius & Hedin (2001) and Hedin *et al.* (2008), is that the average summer temperature was about 2 °C warmer in the field observations of Larsson & Svensson (2009). Flight activity of *O. eremita* is

positively influenced by temperature, both within and among years (Larsson & Svensson, 2011). A comparison of the dispersal biology of *O. eremita* between two regions adds support to this conclusion; using the same methods as Ranius & Hedin (2001) and Hedin *et al.* (2008), Chiari *et al.* (2013) studied *O. eremita* in a considerably warmer site in Italy, and observed higher dispersal rates and ranges. In Sweden, flights were observed only during the warmest part of the day (Ranius *et al.*, 2005), while in Italy flight activity was similar between day and night (Chiari *et al.*, 2013). Thus, dispersal rate and range may be lower for this species at cooler northern locations, but higher in a warmer weather and climate. This implies that metapopulation dynamics for certain species may be more relevant in cooler regions than in warmer, although this has not been tested.

It is difficult to assess dispersal using genetic studies, especially since little is known about current and historical population sizes for invertebrates occupying tree hollows whose genetic structure has been studied. Nevertheless, consistent findings between occurrence patterns and studies of genetic structure strongly support the conclusion that several, but not all, invertebrate species associated with hollow trees have occurrence patterns that are dispersal-limited.

(5) Knowledge gaps

Most research on invertebrates in tree hollows has comprised “snapshots” comparing the fauna in trees with different characteristics. One way to expand our understanding of the ecology of this fauna is to conduct studies at a wider range of spatial and temporal scales. It would be useful to compare large-scale differences in occurrence patterns between regions, and to study the spatial dynamics of species and communities over time. This is particularly relevant from a biodiversity conservation perspective because such studies can increase our understanding of how to mitigate potential negative consequences of climate warming and habitat loss and fragmentation. In addition, greater understanding is needed on the mechanisms giving rise to occurrence patterns, which can reveal how the behaviour of these invertebrates interacts with microclimate, microorganisms, and the chemical properties of tree hollows. Investigations of the interactions among invertebrates in tree hollows also might improve our understanding of their occurrence patterns. Small-scale studies on the mechanisms involved could be conducted in experimental studies in the field and the laboratory.

Much of the research on invertebrates occupying tree hollows has been carried out on oaks, especially in Northern Europe (Fig. 1A). One reason for this bias may be that oaks support more hollows and other microhabitats than many other tree species (Vuidot *et al.*, 2011), and remain standing for a long time after they first develop hollows (Ranius *et al.*, 2009b). Broadening research to other tree species and regions might provide new perspectives on the habitat requirements of invertebrates occupying tree hollows. For instance, for species requiring certain microclimatic conditions, habitat requirements may differ across their geographical range due

to macroclimatic variation. This was observed for saproxylic beetles in downed logs (Gossmann *et al.*, 2024), but has not been studied for species in hollow trees. Hollows in different tree species might differ in variables such as average size, shape, and longevity, which could influence both species occurrence patterns and temporal dynamics.

V. CONCLUSIONS

(1) Hollow-dependent invertebrates are easier to research relative to many other forest and dead wood invertebrates, since their microhabitat is easy to identify. Nevertheless, research on the ecology of this fauna has so far been conducted only in Europe and almost solely on beetles.

(2) Tree hollows buffer climate fluctuations. Tree microclimatic conditions and tree size are important factors explaining habitat suitability.

(3) Metapopulation theory is useful to understand large-scale occurrence patterns and long-term persistence dynamics of invertebrates occupying tree hollows. However, the structure of systems studied to date does not conform to classic metapopulation models, since population sizes vary widely among trees and over time. Instead, the studied metapopulations are habitat-tracking, which means that the temporal dynamics of the trees and the ability of metapopulations to track these dynamics are important factors for understanding the long-term consequences of management and conservation measures.

(4) Prolonging the life of existing hollow trees is an important measure to protect hollow-dependent invertebrate fauna. One reason for this is that hollow trees are typically older and larger than most other trees, but even among hollow trees, the largest trees have higher value, since they have a higher frequency of occurrence of invertebrates associated with hollow trees. In addition, it is critical to ensure recruitment opportunities for new generations of hollow trees (Fig. 1A).

(5) Priority should be given to maintaining or increasing larger clusters of hollow-bearing trees for conserving saproxylic invertebrates that use tree hollows. This is because per-tree use by invertebrates associated with hollow trees is greater in larger clusters of hollow trees relative to single trees or trees in smaller clusters.

(6) To expand our knowledge, it will be useful to compare patterns of occurrence between regions, and study the dynamics of species and communities over time. It will also be useful to understand better how occurrence patterns are influenced by microclimate, microorganisms, and the chemical properties of tree hollows.

VI. REFERENCES

References identified with an asterisk (*) are cited only within the online Supporting Information.
ALEXANDER, K. N. A. (2008). Tree biology and saproxylic Coleoptera: issues of definitions and conservation language. *Revue d'Écologie (La Terre et la Vie)* **63**, 1–5.

- BETTS, M. G., PHALAN, B., FREY, S. J. K., ROUSSEAU, J. S. & YANG, Z. (2018). Old-growth forests buffer climate-sensitive bird populations from warming. *Diversity and Distributions* **24**, 439–447.
- CÁLIX, M., ALEXANDER, K. N. A., NIETO, A., DODELIN, B., SOLDATI, F., TELNOV, D., VAZQUEZ-ALBALADE, X., ALEKSANDROWICZ, O., AUDISIO, P., ISTRATE, P., JANSSON, N., LEGARIS, A., LIBERTO, A., MAKRIS, C., MERKL, O., *ET AL.* (2018). *European Red List of Saproxylic Beetles*. IUCN, Brussels.
- CARLSSON, S., BERGMAN, K.-O., JANSSON, N., RANIUS, T. & MILBERG, P. (2016). Boxing for biodiversity: evaluation of an artificially created decaying wood habitat. *Biodiversity and Conservation* **25**, 393–405.
- CARPANETO, G. M., MAZZIOTTA, A., COLETTI, G., LUISELLI, L. & AUDISIO, P. (2010). Conflict between insect conservation and public safety: the case of a saproxylic beetle (*Osmoderma eremita*) in urban parks. *Journal of Insect Conservation* **14**, 555–565.
- CHIARI, S., CARPANETO, G. M., ZAULI, A., MARINI, L. & RANIUS, T. (2012). Habitat of an endangered saproxylic beetle, *Osmoderma eremita*, in Mediterranean woodlands. *Écoscience* **19**, 299–307.
- CHIARI, S., CARPANETO, G. M., ZAULI, A., ZIRPOLI, G. M., AUDISIO, P. & RANIUS, T. (2013). Dispersal patterns of a saproxylic beetle, *Osmoderma eremita*, in Mediterranean woodlands. *Insect Conservation and Diversity* **6**, 309–318.
- COCKLE, K. L., MARTIN, K. & WESOŁOWSKI, T. (2011). Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Frontiers in Ecology and the Environment* **9**, 377–382.
- *DELLA ROCCA, F., JANSSON, N., CHIARI, S., ZAULI, A. & CARPANETO, G. M. (2023). Micro-habitat drivers of saproxylic beetle assemblages in old woodlands of Mediterranean cork oak (*Quercus suber*). *Agricultural and Forest Entomology* **25**, 77–90.
- *DUBOIS, G. & VIGNON, V. (2008). First results of radio-tracking of *Osmoderma eremita* (Coleoptera: Cetoniidae) in French chestnut orchards. *Revue d'Écologie (la Terre et la Vie)* **63**, 131–138.
- ELTZ, T., BRÜHL, C. A., IMIYABIR, Z. & LINSSEMAIR, K. E. (2003). Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, with implications for forest management. *Forest Ecology and Management* **172**, 301–313.
- FAHRIG, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* **34**, 487–515.
- FAHRIG, L., WATLING, J. I., ARNILLAS, C. A., ARROYO-RODRÍGUEZ, V., JÖRGER-HICKFANG, T., MÜLLER, J., PEREIRA, H. M., RIVA, F., RÖSCH, V., SEIBOLD, S., TSCHARNTKE, T. & MAY, F. (2021). Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. *Biological Reviews* **97**, 99–114.
- GIBBONS, P. & LINDENMAYER, D. (2002). *Tree Hollows and Wildlife Conservation in Australia*. CSIRO Publishing, Collingwood.
- GIBBONS, P., LINDENMAYER, D. B., FISCHER, J., MANNING, A. D., WEINBERG, A., SEDDON, J., RYAN, P. & BARRATT, G. (2008). The future of scattered trees in agricultural landscapes. *Conservation Biology* **22**, 1309–1319.
- GIBBONS, P., McELHINNY, C. & LINDENMAYER, D. B. (2010). What strategies are effective for perpetuating structures provided by old trees in harvested forests? A case study on trees with hollows in south-eastern Australia. *Forest Ecology and Management* **260**, 975–982.
- *GOUGH, L. A., BIRKEMOE, T. & SVERDRUP-THYGESON, A. (2014). Reactive forest management can also be proactive for wood-living beetles in hollow oak trees. *Biological Conservation* **180**, 75–83.
- GOUTX, N., SEBEK, P., VALLADARES, L., BRUSTEL, H. & BRIN, A. (2015). Habitat requirements of the violet click beetle (*Limonicus violaceus*), an endangered umbrella species of basal hollow trees. *Insect Conservation and Diversity* **8**, 418–427.
- GOSSMANN, A., ÖCKINGER, E., SCHROEDER, M., LINDMAN, L. & RANIUS, T. (2024). Interaction between regional temperature and shade level shapes saproxylic beetle communities. *Diversity and Distributions* **30**, e13836.
- HAGGE, J., MÜLLER, J., BIRKEMOE, T., BUSE, J., CHRISTENSEN, R. H. B., GOSSNER, M. M., GRUPPE, A., HEIBL, C., JARZABEK-MÜLLER, A., SEIBOLD, S., SIITONEN, J., SOUTINHO, J. G., SVERDRUP-THYGESON, A., THORN, S. & DRAG, L. (2021). What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. *Journal of Animal Ecology* **90**, 1934–1947.
- HARRISON, S. & TAYLOR, A. D. (1997). Empirical evidence for metapopulation dynamics. In *Metapopulation Biology. Ecology, Genetics, and Evolution* (eds I. HANSKI and M. E. GILPIN), pp. 27–42. Academic Press, London.
- HARTEL, T., DORRESTEIJN, I., KLEIN, C., MÁTHÉ, O., MOGA, C. I., ÖLLERER, K., ROELLIG, M., VON WEHRDEN, J. & FISCHER, J. (2013). Wood-pastures in a traditional rural region of Eastern Europe: characteristics, management and status. *Biological Conservation* **166**, 267–275.
- HEDIN, J., RANIUS, T., NILSSON, S. G. & SMITH, H. G. (2008). Restricted dispersal in a flying beetle assessed by telemetry. *Biodiversity and Conservation* **17**, 675–684.
- HENNEBERG, B., BAUER, S., BIRKENBACH, M., MERTL, V., STEINBAUER, M. J., FELDHAAR, H. & OBERMAIER, E. (2021). Influence of tree hollow characteristics and forest structure on saproxylic beetle diversity in tree hollows in managed forests in a regional comparison. *Ecology and Evolution* **11**, 17973–17999.

- HERNÁNDEZ-CORRAL, J., GARCÍA-LÓPEZ, A., FERRÁNDEZ, M. Á. & MICÓ, E. (2021). Physical and biotic factors driving the diversity of spider assemblages in tree hollows of Mediterranean *Quercus* forests. *Insect Conservation and Diversity* **14**, 515–526.
- JANSSON, N., RANIUS, T., LARSSON, A. & MILBERG, P. (2009). Boxes mimicking tree hollows can help conservation of saproxylic beetles. *Biodiversity and Conservation* **18**, 3891–3908.
- JOHANSSON, V., RANIUS, T. & SNÄLL, T. (2012). Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics. *Ecology* **93**, 235–241.
- JONSELL, M. (2012). Old park trees as habitat for saproxylic beetle species. *Biodiversity and Conservation* **21**, 619–642.
- JÖNSSON, N., MÉNDEZ, M. & RANIUS, T. (2004). Nutrient richness of wood mould in tree hollows with the Scarabaeid beetle *Osmoderma eremita*. *Animal Biodiversity and Conservation* **27**(2), 79–82.
- KADEJ, M., ZAJĄC, K., SMOLIS, A., TARNAWSKI, D. & MALKIEWICZ, A. (2016). Isolation from forest habitats reduces chances of the presence of *Osmoderma eremita* sensu lato (Coleoptera: Scarabaeidae) in rural avenues. *Journal of Insect Conservation* **20**, 395–406.
- KATANO, I., DOI, H., ERIKSSON, B. K. & HILLEBRAND, H. (2015). A cross-system meta-analysis reveals coupled predation effects on prey biomass and diversity. *Oikos* **124**, 1427–1435.
- KOZÁK, D., SVITOK, M., ZEMLEROVÁ, V., MIKOLÁŠ, M., LACHAT, T., LARRIEU, L., PAILLET, Y., BUECHLING, A., BAČE, R., KEETON, W. S., VÍTKOVÁ, L. & BEGOVIĆ, K. (2023). Importance of conserving large and old trees to continuity of tree-related microhabitats. *Conservation Biology* **37**, e14066.
- LANDE, R. (1987). Extinction thresholds in demographic models of territorial populations. *American Naturalist* **130**, 624–635.
- LANDVIK, M., NIEMELÄ, P. & ROSLIN, T. (2016a). Mother knows the best mould: an essential role for non-wood dietary components in the life cycle of a saproxylic scarab beetle. *Oecologia* **182**, 163–175.
- *LANDVIK, M., NIEMELÄ, P. & ROSLIN, T. (2016b). Opportunistic habitat use by *Osmoderma barnabita* (Coleoptera: Scarabaeidae), a saproxylic beetle dependent on tree cavities. *Insect Conservation and Diversity* **9**, 38–48.
- LAROCHE, F., PALTTO, H. & RANIUS, T. (2018). Abundance-based detectability in a spatially explicit metapopulation: a case study on a vulnerable beetle species in hollow trees. *Oecologia* **188**, 671–682.
- LARSSON, M. C. & SVENSSON, G. P. (2009). Pheromone monitoring of rare and threatened insects: exploiting a pheromone-kairomone system to estimate prey and predator abundance. *Conservation Biology* **23**, 1516–1525.
- LARSSON, M. C. & SVENSSON, G. P. (2011). Monitoring spatiotemporal variation in abundance and dispersal by a pheromone-kairomone system in the threatened saproxylic beetles *Osmoderma eremita* and *Elater ferrugineus*. *Journal of Insect Conservation* **15**, 891–902.
- LARSSON, M. C., HEDIN, J., SVENSSON, G. P., TOLASCH, T. & FRANCKE, W. (2003). Characteristic odor of *Osmoderma eremita* identified as a male-released pheromone. *Journal of Chemical Ecology* **29**, 575–587.
- LE ROUX, D. S., IKIN, K., LINDENMAYER, D. B., MANNING, A. D. & GIBBONS, P. (2014). The future of large old trees in urban landscapes. *PLoS One* **9**, e99403.
- LE ROUX, D. S., IKIN, K., LINDENMAYER, D. B., MANNING, A. D. & GIBBONS, P. (2018). The value of scattered trees for wildlife: contrasting effects of landscape context and tree size. *Diversity and Distributions* **24**, 69–81.
- LINDENMAYER, D. B. & LAURANCE, W. F. (2017). The ecology, distribution, conservation and management of large old trees. *Biological Reviews* **92**, 1434–1458.
- LINDENMAYER, D. B., LAURANCE, W. F. & FRANKLIN, J. F. (2012). Global decline in large old trees. *Science* **338**, 1305–1306.
- LINDMAN, L., LARSSON, M. C., MELLBRAND, K., SVENSSON, G. P., HEDIN, J., TRANBERG, O. & RANIUS, T. (2020). Metapopulation dynamics over 25 years of a beetle, *Osmoderma eremita*, inhabiting hollow oaks. *Oecologia* **194**, 771–780.
- LINDMAN, L., ÖCKINGER, E. & RANIUS, T. (2022). Microclimatic conditions mediate the effect of deadwood and forest characteristics on a threatened beetle species, *Tragosoma depasarium*. *Oecologia* **199**, 737–752.
- LINDMAN, L., ÖCKINGER, E. & RANIUS, T. (2023). Microclimate in hollow trees and how it affects an inhabiting beetle species, *Osmoderma eremita*. *Ecological Entomology* **48**, 112–126.
- MANNING, A. D., FISCHER, J. & LINDENMAYER, D. B. (2006). Scattered trees are keystone structures – implications for conservation. *Biological Conservation* **132**, 311–321.
- MCLEAN, C. M., BRADSTOCK, R., OWEN, P. & KAVANAGH, R. P. (2015). Tree hollows and forest stand structure in Australian warm temperature *Eucalyptus* forests are adversely affected by logging more than wildfire. *Forest Ecology and Management* **341**, 37–44.
- MESTRE, L., JANSSON, N. & RANIUS, T. (2018). Saproxylic biodiversity and decomposition rate decrease with small-scale isolation of tree hollows. *Biological Conservation* **227**, 226–232.
- MICÓ, E. (2018). Saproxylic insects in tree hollows. In *Saproxylic Insects. Diversity, Ecology And Conservation. Zoological Monographs* (Volume 1, ed. M. D. ULYSHEN), pp. 693–727. Springer, Berlin.
- *MICÓ, E., GARCÍA-LÓPEZ, A., SÁNCHEZ, A., JUÁREZ, M. & GALANTE, E. (2015). What can physical, biotic and chemical features of a tree hollow tell us about their associated diversity? *Journal of Insect Conservation* **19**, 144–153.
- MILBERG, P., BERGMAN, K.-O., JOHANSSON, H. & JANSSON, N. (2014). Low host tree preferences among saproxylic beetles: a comparison of four deciduous species. *Insect Conservation and Diversity* **7**, 508–522.
- MILBERG, P., BERGMAN, K.-O., SANGAK, K. & JANSSON, N. (2016). Assemblages of saproxylic beetles on large downed trunks of oak. *Ecology and Evolution* **6**, 1614–1625.
- MITRUS, S., HEBDA, G. & WESOŁOWSKI, T. (2016). Cohabitation of tree holes by ants and breeding birds in a temperate deciduous forest. *Scandinavian Journal of Forest Research* **31**, 135–139.
- MUSA, N., ANDERSSON, K., BURMAN, J., ANDERSSON, F., HEDENSTRÖM, E., JANSSON, N., PALTTO, H., WESTERBERG, L., WINDE, I., LARSSON, M. C., BERGMAN, K.-O. & MILBERG, P. (2013). Using sex pheromone and a multi-scale approach to predict the distribution of a rare saproxylic beetle. *PLoS One* **8**, e66149.
- NILSSON, S. G. & BARANOWSKI, R. (1997). Habitat predictability and the occurrence of wood beetles in old-growth beech forests. *Ecography* **20**, 491–498.
- NILSSON, S. G., NIKLASSON, M., HEDIN, J., ELIASSON, P. & LJUNGBERG, H. (2006). Biodiversity and sustainable forestry in changing landscapes – principles and southern Sweden as an example. *Journal of Sustainable Forestry* **21**, 11–43.
- NOLAN, V., READER, T., GILBERT, F. & ATKINSON, N. (2020). The Ancient Tree Inventory: a summary of the results of a 15 year citizen science project recording ancient, veteran and notable trees across the UK. *Biodiversity and Conservation* **29**, 3103–3129.
- *OLEKSA, A., ULRICH, W. & GAWROŃSKI, R. (2006). Occurrence of the marbled rose-chaffer (*Protaetia lugubris* Herbst, Coleoptera, Cetoniidae) in rural avenues in northern Poland. *Journal of Insect Conservation* **10**, 241–247.
- *OLEKSA, A., ULRICH, W. & GAWROŃSKI, R. (2007). Host tree preferences of hermit beetles (*Osmoderma eremita* Scop., Coleoptera: Scarabaeidae) in a network of rural avenues in Poland. *Polish Journal of Ecology* **55**, 315–323.
- OLEKSA, A., CHYBICKI, I. J., GAWROŃSKI, R., SVENSSON, G. P. & BURCZYK, J. (2013). Isolation by distance in saproxylic beetles may increase with niche specialization. *Journal of Insect Conservation* **17**, 219–233.
- OLEKSA, A., CHYBICKI, I. J., LARSSON, M. C., SVENSSON, G. P. & GAWROŃSKI, R. (2015). Rural avenues as dispersal corridors for the vulnerable saproxylic beetle *Elater ferrugineus* in a fragmented agriculture landscape. *Journal of Insect Conservation* **19**, 567–580.
- OMLIN, F. X., CARLSON, J. C., OGBUNUGAFO, C. B. & HASSANALI, A. (2007). *Anopheles gambiae* exploits the treehole ecosystem in western Kenya: a new urban malaria risk? *American Journal of Tropical Medicine and Hygiene* **77**, 264–269.
- PALM, T. (1959). Die Holz- und Rinden-käfer der Süd- und Mittelschwedischen Laubbäume. *Opuscula Entomologica Supplementum* **16**, 374.
- PARMAIN, G. & BOUGET, C. (2018). Large solitary oaks as keystone structures for saproxylic beetles in European agricultural landscapes. *Insect Conservation and Diversity* **11**, 100–115.
- PARSONS, C. R., CUNNINGHAM, S., LE ROUX, D. S. & GIBBONS, P. (2023). The impact of greenfield residential development on mature trees. *Urban Forestry and Urban Greening* **86**, 128006.
- PAUTASSO, M., AAS, G., QUELOZ, V. & HOLDENRIEDER, O. (2013). European ash (*Fraxinus excelsior*) dieback – a conservation biology challenge. *Biological Conservation* **158**, 37–49.
- PERCEL, G., LAROCHE, F. & BOUGET, C. (2019). The scale of saproxylic beetles response to landscape structure depends on their habitat suitability. *Landscape Ecology* **34**, 1905–1918.
- PETERMANN, J. S. & GOSSNER, M. M. (2022). Aquatic islands in the sky: 100 years of research on water-filled tree holes. *Ecology and Evolution* **12**, e9206.
- PILSKOG, H. E., BIRKEMOE, T., FRAMSTAD, E. & SVERDRUP-THYGESON, A. (2016). Effect of habitat size, quality, and isolation on functional groups of beetles in hollow oaks. *Journal of Insect Science* **16**, 24.
- PILSKOG, H. E., SVERDRUP-THYGESON, A., EVJU, M., FRAMSTAD, E. & BIRKEMOE, T. (2018). Long-lasting effects of logging on beetles in hollow oaks. *Ecology and Evolution* **8**, 10126–10137.
- QUINTO, J., MICÓ, E., MARTÍNEZ-FALCÓN, A. P., GALANTE, E. & MARCOS-GARCÍA, M. Á. (2014). Influence of tree hollow characteristics on the diversity of saproxylic insect guilds in Iberian Mediterranean woodlands. *Journal of Insect Conservation* **18**, 981–992.
- *RANIUS, T. (2000). Minimum viable metapopulation size of a beetle, *Osmoderma eremita*, living in tree hollows. *Animal Conservation* **3**, 37–43.
- RANIUS, T. (2001). Constancy and asynchrony of *Osmoderma eremita* populations in tree hollows. *Oecologia* **126**, 208–215.
- RANIUS, T. (2002). Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biological Conservation* **103**, 85–91.
- RANIUS, T. (2007). Extinction risks in metapopulations of a beetle inhabiting hollow trees predicted from time series. *Ecography* **30**, 716–726.
- RANIUS, T., AGUADO, L. O., ANTONSSON, K., AUDISIO, P., BALLERIO, A., CARPANETO, G. M., CHOBOT, K., GJURAŠIN, B., HANSSON, O.,

- HUIJBREGTS, H., LAKATOS, F., MARTIN, O., NECULISEANU, Z., NIKITSKY, N. B., PAILLÉ, W., ET AL. (2005). *Osmoderma eremita* (Coleoptera, Scarabaeidae, Cetoniinae) in Europe. *Animal Biodiversity and Conservation* **28**(1), 1–44.
- RANIUS, T. & DOUWES, P. (2002). Genetic structure of two pseudoscorpion species living in tree hollows in Sweden. *Animal Biodiversity and Conservation* **25**(2), 67–74.
- RANIUS, T., GROVE, S., LINDENMAYER, D. & SIITONEN, J. (2024). Invertebrates in large old trees. In *Large and Old Trees – Ecological and Cultural Significance* (eds M. Blicharska, G. Mikusinski and D. Lindenmayer). Springer Nature, Berlin.
- RANIUS, T. & HEDIN, J. (2001). The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia* **126**, 363–370.
- RANIUS, T. & JANSSON, N. (2000). The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation* **95**, 85–94.
- *RANIUS, T., JOHANSSON, V. & FAHRIG, L. (2010). A comparison of patch connectivity measuring data on invertebrates in hollow oaks. *Ecography* **33**, 971–978.
- RANIUS, T., JOHANSSON, V. & FAHRIG, L. (2011). Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden. *Biodiversity and Conservation* **20**, 2027–2040.
- RANIUS, T., NIKLASSON, M. & BERG, N. (2009a). Development of tree hollows in pedunculate oak (*Quercus robur*). *Forest Ecology and Management* **257**, 303–310.
- RANIUS, T. & NILSSON, S. G. (1997). Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabaeidae), a beetle living in hollow trees. *Journal of Insect Conservation* **1**, 193–204.
- RANIUS, T., SVENSSON, G. P., BERG, N., NIKLASSON, M. & LARSSON, M. C. (2009b). The successional change of hollow oaks affects their suitability for an inhabiting beetle, *Osmoderma eremita*. *Annales Zoologici Fennici* **46**, 205–216.
- RANIUS, T. & WILANDER, P. (2000). Occurrence of *Larva lata* H.J. Hansen (Pseudoscorpionida: Garypidae) and *Allochemes wideri* C.L. Koch (Pseudoscorpionida: Chernetidae) in tree hollows in relation to habitat quality and density. *Journal of Insect Conservation* **4**, 23–31.
- SÁNCHEZ-GALVÁN, I. R., QUINTO, J., MICÓ, E., GALANTE, E. & MARCOS-GARCÍA, M. A. (2014). Facilitation among saproxylic insects inhabiting tree hollows in a Mediterranean forest: the case of cetonids (Coleoptera: Cetoniidae) and syrphids (Diptera: Syrphidae). *Environmental Entomology* **43**, 336–343.
- SÁNCHEZ, A., MICÓ, E., GALANTE, E. & JUÁREZ, M. (2017). Chemical transformation of *Quercus* wood by *Cetonia* larvae (Coleoptera: Cetoniidae): an improvement of carbon and nitrogen available in saproxylic environments. *European Journal of Soil Biology* **78**, 57–65.
- SCHAUER, B., BONG, J., POPP, C., OBERMAIER, E. & FELDHAAR, H. (2018a). Dispersal limitation of saproxylic insects in a managed forest? A population genetics approach. *Basic and Applied Ecology* **32**, 26–38.
- SCHAUER, B., STEINBAUER, M. J., VAILSHERY, L. S., MÜLLER, M., FELDHAAR, H. & OBERMEIER, E. (2018b). Influence of tree hollow characteristics on saproxylic beetle diversity in managed forest. *Biodiversity and Conservation* **27**, 853–869.
- SIITONEN, J. & RANIUS, T. (2015). The importance of veteran trees for saproxylic insects. In *Europe's Changing Woods and Forests: From Wildwood to Cultural Landscapes* (eds K. J. Kirby and C. Watkins), pp. 183–191. CABI, Oxfordshire.
- *SKARPAAS, O., DISERUD, O. H., SVERDRUP-THYGESON, A. & ØDEGAARD, F. (2011). Predicting hotspots for red-listed species: multivariate regression models for oak-associated beetles. *Insect Conservation and Diversity* **4**, 53–59.
- SVENSSON, G. P., LARSSON, M. C. & HEDIN, J. (2004). Attraction of the larval predator *Elater ferrugineus* to the sex pheromones of its prey, *Osmoderma eremita*, and its implication for conservation biology. *Journal of Chemical Ecology* **30**, 353–363.
- SVENSSON, G. P., SAHLIN, U., BRAGE, B. & LARSSON, M. C. (2011). Should I stay or should I go? Modelling dispersal strategies in saproxylic insects based on pheromone capture and radio telemetry: a case study on the threatened hermit beetle *Osmoderma eremita*. *Biodiversity and Conservation* **20**, 2883–2902.
- SVERDRUP-THYGESON, A., SKARPAAS, O. & ØDEGAARD, F. (2010). Hollow oaks and beetle conservation: the significance of the surroundings. *Biodiversity and Conservation* **19**, 837–852.
- THOMAS, C. D., THOMAS, J. A. & WARREN, M. S. (1992). Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* **92**, 563–567.
- *VALAINIS, U., NITCIS, M., AKSJUTA, K., BARŠEVSKIS, A., CIBUŠKIS, R., BALALAIKINS, M. & AVGIN, S. S. (2015). Results of using pheromone-baited traps for investigations of *Osmoderma bamabita* Motschulsky, 1845 (Coleoptera: Scarabaeidae: Cetoniinae) in Latvia. *Baltic Journal of Coleopterology* **15**, 37–46.
- UIDOT, A., PAILLET, Y., ARCHAU, F. & GOSSELIN, F. (2011). Influence of tree characteristics and forest management on tree microhabitats. *Biological Conservation* **144**, 441–450.
- WALKER, E. D. & MERRITT, R. W. (1988). The significance of leaf detritus to mosquito (Diptera: Culicidae) productivity from treeholes. *Environmental Entomology* **17**, 199–206.
- WETHERBEE, R., BIRKEMOE, T., SKARPAAS, O. & SVERDRUP-THYGESON, A. (2020a). Hollow oaks and beetle functional diversity: significance of surroundings extends beyond taxonomy. *Ecology and Evolution* **10**, 819–831.
- WETHERBEE, R., BIRKEMOE, T. & SVERDRUP-THYGESON, A. (2020b). Veteran trees are a source of natural enemies. *Scientific Reports* **10**, 18485.
- WETHERBEE, R., BIRKEMOE, T., BURNER, R. C. & SVERDRUP-THYGESON, A. (2021). Veteran trees have divergent effects on beetle diversity and wood decomposition. *PLoS One* **16**, e0248756.
- WETHERBEE, R., BIRKEMOE, T., ASPLUND, J., RENČO, M. & SVERDRUP-THYGESON, A. (2022). It takes a community to maintain a tree hollow: food web complexity enhances decomposition and wood mould production. *Functional Ecology* **36**, 2215–2226.
- WOOLLEY, L.-A., MURPHY, B. P., RADFORD, I. J., WESTAWAY, J. & WOJNARSKI, J. C. (2018). Cyclones, fire, and termites: the drivers of tree hollow abundance in northern Australia's mesic tropical savanna. *Forest Ecology and Management* **419**, 146–159.

VII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Relevant papers found in our literature search, divided according to which of our questions they contributed answers to.

Table S2. Data compiled in Table 2.

(Received 29 September 2023; revised 27 May 2024; accepted 31 May 2024; published online 10 June 2024)