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ISOLATED IN THE LAST REFUGIUM
– The Identity, Ecology and Conservation of the
Northernmost Occurrence of the Hermit Beetle

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"The four stages of acceptance:

1. This is worthless nonsense.

2. This is an interesting, but perverse, point of view.

3. This is true, but quite unimportant.

4. I always said so."

— J.B.S. Haldane
J. Genet. 1963. Vol. 58, p.464

ABSTRACT

The hermit beetle (*Osmoderma eremita* sensu lato) is a flagship species for invertebrate conservation in Europe. Protecting this species will also aid in the preservation of other saproxylic communities on veteran trees. However, the European hermit beetle is not a single species but comprises at least four cryptic species, the distribution, morphology, and genetics of which have diverged from each other. In the current thesis, I focus on the hermit beetle in Finland. My work had five objectives: First, to establish the species identity of the Finnish population, which was previously unclear. Second, to retrace the origin and demographic history of this population with the aid of a genetic marker. Third, to establish the current range of the species in Finland. Fourth, to study its habitat requirements within its Finnish range. Fifth, within its habitat, to dissect the species' larval substrate requirements. Overall, I hoped to derive clear-cut recommendations for the conservation of this threatened species in its northernmost range.

With respect to its taxonomic affinity, the Finnish population of the hermit beetle turned out to belong to the eastern clade of *O. eremita* s.l., more specifically to *Osmoderma barnabita* Motschulsky, 1845 (syn. *O. coriarium*). In terms of variation within the mitochondrial *COI* gene, the Finnish population proved to be characterised by very low genetic variation. Overall, the diversity of the *COI* marker was found to decrease northwards of Central and Eastern Europe, a pattern which may be attributed to post-glacial migration. In Finland, the occurrence of the species was confirmed to be restricted to the Turku region, with Ruissalo Island being the core of its distribution. The eastern clade hermit beetle species has not been recorded in any other part of Fennoscandia.

Within its Finnish range, the hermit beetle occurred most frequently within large-sized hollow oaks (*Quercus robur*), of which the species occupied ca 90 %. Nevertheless, the beetle was encountered in hollows of multiple different tree species (*Tilia* sp., *Alnus glutiosa*, *Acer platanoides*, *Sorbus aucuparia*), and consequently, conservation should not be focused on particular tree species. Neither the specific location of the tree (e.g. open area, dense forest) nor the characteristics of the cavity (e.g. the size of the entrance hole, the volume of wood mould) had any clear-cut effect on the presence of the species. Thus, the species seems fairly liberal in terms of its habitat requirements.

Within their habitat, the larvae of the hermit beetle develop on a substrate consisting of decaying organic material. Here, a high content of nutrient-rich leaf humus was observed to promote both larval growth and female oviposition, whereas the material of the cavity walls, including brown-rot wood and mycelium of the sulphur polypore (*Laetiporus sulphureus*), were of inferior quality as regards larval development. A link between female preference and larval performance indicates that female beetles are able to detect the quality of their oviposition site for their larvae.

Overall, my results suggest that the regional populations should be managed as separate subunits, and that the northernmost, Finnish population of *O. barnabita* may be marked by low total genetic diversity. The conservation management of this population should be focused on securing a continuous supply of veteran trees, and large-sized broadleaf trees should be retained regardless of the tree species. As hermit beetle presence on host trees is often difficult to establish, more effort should be invested in the strategic, long-term maintenance of a good supply of hollow trees than in the *ad hoc* rescue of single tree-level occurrences. Furthermore, study of the hollow substrates should continue as the results can be beneficial in improving the future habitat quality of the hermit beetle.

TIIVISTELMÄ

Erakkokuoriainen (*Osmoderma eremita* sensu lato) on selkärangattomien eläinten lajisuojelun lippulaivalaji Euroopassa, jonka suojelu edesauttaa myös veteraanipuita hyödyntävien eliöyhteisöjen säilyttämistä. Euroopan erakkokuoriainen ei kuitenkaan ole yksittäinen laji, vaan se muodostaa vähintään neljä kryptistä lajia, joiden levinneisyys, morfologia ja perimä ovat eriytyneet toisistaan. Tässä väitöstutkimuksessa huomioni keskittyy erakkokuoriaisen esiintymään Suomessa. Minulla on viisi päämäärää: Ensiksi pyrin selvittämään suomalaisen erakkokuoriaispopulaation lajin. Toiseksi, jäljitän tuon populaation alkuperän ja demografisen historian geenimarkkeria hyödyntäen. Kolmanneksi, varmistan erakkokuoriaisen levinneisyyden laajuuden Suomessa. Neljänneksi, tutkin lajin habitaattivaatimukset Suomessa. Viidenneksi, tarkastelen lajin vaatimuksia toukkien ravinnonkäytön osalta. Kaiken kaikkiaan toivon tutkimukseni tuottavan selkeät suositukset tämän uhanalaisen lajin suojelulle sen pohjoisimmalla esiintymisalueella.

Taksonomisesti erakkokuoriaisen Suomen populaatio osoittautui kuuluvan *Osmoderma eremita* s.l. itäiseen lajiryhmään, ja tarkemmin *Osmoderma barnabita* Motschulsky, 1845 (syn. *O. coriarium*). Mitokondrion *COI*-geenin osalta Suomen populaation geneettinen variaatio oli vähäistä. Lajin *O. barnabita COI*-markkerin diversiteetti väheni pohjoissuuntaisesti Keski- ja Itä-Euroopasta, mikä on todennäköisimmin seuraus post-glasiaalisesta migraatiosta. Suomessa lajin levinneisyysalueeksi varmistui Turun seutu, jossa Ruissalon saari on esiintymän ydin. Itäistä erakkokuoriaislajia ei tunneta muualta Fennoskandiasta.

Suomen päälevinneisyysalueella erakkokuoriainen esiintyi useimmiten suurikokoisten tammien (*Quercus robur*) onkaloissa, joissa lajin esiintyvyys oli noin 90 % tasolla. Kuoriaislajia tavattiin kuitenkin useampien puulajien (*Tilia* sp., *Alnus glutiosa*, *Acer platanoides*, *Sorbus aucuparia*) onkaloista, joten lajisuojelu ei tulisi perustua ainoastaan tiettyihin puulajeihin. Myöskään yksittäisen puun sijainti (esim. avoin ympäristö, tiheä metsä), tai puun onkalon ominaisuudet (esim. aukon koko, puuhumuksen määrä) eivät vaikuttaneet merkittävästi lajin esiintyvyyteen. Näin ollen lajin vaatimukset habitaattinsa osalta vaikuttavat melko väljiltä.

Habitaatissaan erakkokuoriaisen toukat kehittyvät lahoavassa substraatissa, joka koostuu orgaanisesta materiaalista. Tutkimuksessa substraattiin sisältyneen runsasravinteisen lehtihumuksen suuren määrän havaittiin edistävän toukkien kasvua ja naaraiden munintaa. Sen sijaan lahopuiden onkaloiden seinämän materiaali, punalahopuu ja rikkikäävän (*Laetiporus sulphureus*) sienirihmasto, todettiin huonolaatuiseksi toukkien kehittymiselle. Naaraiden muninnan ja toukkien kasvun välinen yhteys viittaa naaraiden kykyyn arvioida munintapaikkansa laatu toukkiensa kasvuvaatimusten kannalta.

Tulokseni osoittavat, että erakkokuoriaisen toisistaan etäällä sijaitsevien osapopulaatioiden suojelutoimet tulisi toteuttaa erillisinä, ja että pohjoisimman, suomalaisen *O. barnabita* populaation geneettinen diversiteetti saattaa olla vähäistä. Tämän erakkokuoriaispopulaation suojelussa tulisi turvata veteraanipuiden jatkuva saatavuus esiintymäalueella, ja suurikokoiset lehtipuut pitäisi säilyttää niiden puulajista huolimatta. Erakkokuoriaisen käyttämien puiden vaikean todennettavuuden seurauksena lajisuojelun strategiana tulisikin painottaa onkalopuiden suuren määrän säilyttämistä pitkällä aikavälillä yksittäisten puiden *ad hoc* suojelun sijaan. Lisäksi tutkimuksia onkalopuiden substraattien vaikutuksista tulisi jatkaa, koska tuloksia voidaan tulevaisuudessa hyödyntää erakkokuoriaisen habitaatin laadun edistämisessä.

TABLE OF CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The current thesis consists of the following publications and manuscript, referred to by Roman numerals in the text.

I.   Landvik M, Wahlberg N, Roslin T (2013) The identity of the Finnish *Osmoderma* (Coleoptera: Scarabaeidae, Cetoniinae) population established by COI sequencing. *Entomologica Fennica* 24 (3):147–155

II.   Landvik M*, Miraldo A*, Niemelä P, Valainis U, Cibuļskis R, Roslin T (2017) Evidence for geographic substructuring of mtDNA variation in the East European Hermit beetle (*Osmoderma barnabita*). *Nature Conservation* 19:171-189 doi 10.3897/natureconservation.19.12877

III.   Landvik M, Niemelä P, Roslin T (2016) Opportunistic habitat use by *Osmoderma barnabita* (Coleoptera: Scarabaeidae), a saproxylic beetle dependent on tree cavities. *Insect Conservation and Diversity* 9 (1):38–48 doi 10.1111/icad.12141

IV.   Landvik M, Niemelä P, Roslin T (2016) Mother knows the best mould: an essential role for non-wood dietary components in the life cycle of a saproxylic scarab beetle. *Oecologia* 182 (1):163-175 doi 10.1007/s00442-016-3661-y

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1.   INTRODUCTION

The hermit beetle *Osmoderma eremita* (Scopoli, 1763) is a flagship species in European conservation biology. Its high status assists in protecting larger communities of threatened species on veteran trees (Anonymous 1992; Ranius 2002a; European Commission 2007). The life cycle of the hermit beetle has been connected especially to pedunculate oak *Quercus robur* L. in Northern Europe (Palm 1959; Ranius & Nilsson 1997), but its host trees vary substantially across Europe (Ranius *et al*. 2005). Taxonomical studies have revealed the existence of a western and an eastern clade within the European species complex of *Osmoderma eremita* sensu lato. These clades comprise at least four separate species in the genus (Gusakov 2002; Löbl & Smetana 2006; Audisio *et al*. 2007).

In the latest Finnish Red List (Rassi *et al*. 2010), the hermit beetle was evaluated as belonging to species *Osmoderma eremita* sensu stricto within the western clade, but no specimens from Finland have been included in previous reviews based on morphology (Tauzin 1994a; Tauzin 1994b; Krell 1996; Sparacio 2000; Gusakov 2002) and DNA analysis (Audisio *et al*. 2009; Svensson *et al*. 2009). Audisio *et al*. (2007, 2009) propose that the Finnish hermit beetle belongs to species *Osmoderma barnabita* s.s. within the eastern clade, due to its hypothetical migration route. Similarly, the International Union for Conservation of Nature (IUCN), has presented a map with a wide distribution of *O. barnabita* in South Western Finland including the Åland Islands, with small fragmented populations along the South coast (cf. Alexander *et al*. 2010). Nevertheless, only a single population is known from Finland, occurring in the Turku region (Landvik 2000; Mannerkoski 2001), and the closest neighbouring populations which are on the East coast of Sweden have been identified as belonging to *O. eremita* s.s. within the western clade (Antonsson *et al*. 2003; Ranius *et al*. 2005; Audisio *et al*. 2009).

Establishing the true species affinity of the Finnish population is clearly a priority, since habitat requirements may differ among the separate species of the *Osmoderma* species complex (cf. Ranius *et al*. 2005; Siitonen & Ranius 2016). To promote the conservation of the species, this doctoral thesis aims to establish the taxonomical status, demographic history, distribution, habitat characteristics, and habitat use of the hermit beetle in Finland.

1.1   The species complex *Osmoderma eremita* sensu lato

The hermit beetle genus *Osmoderma* LePeletier & Audinet-Serville, 1828 (Scarabaeidae: Cetoniinae) consists of four accepted species in Europe (Löbl & Smetana 2006; Audisio *et al*. 2007; Schoolmeesters 2017). This genus was traditionally assigned to the subtribe Osmodermatina (two genera) of the tribe Trichiini, a large clade of Cetoniinae that

Fig. 1. Taxa within the cryptic species complex of European *Osmoderma* show similarities in larval and adult beetle morphology, as well in optimal habitat characteristics: (a) the imagos are large-sized, metallic-brown beetles with a clear sexual dimorphism (male on the left, and female on the right); (b) the larvae are typical scarabaeiforms living in the wood mould of tree cavities; and (c) the host trees are usually located in open cultural landscapes with a previous history of management. Photographs © Matti Landvik.

includes the widespread genera *Trichius*, *Gnorimus* and others (Schoolmeesters 2017). However, recent molecular study (Šípek *et al*. 2016) suggested closer affinities between *Osmoderma* and other fruit chafers, more than with the above-mentioned genera and thus concluding that it should be assigned to the tribe Cetoniini. The adult of *Osmoderma eremita* s.l. is a large-sized (20–39 mm) dark beetle (Fig. 1a), with a metallic brown lustre on its chitin (cf. Freude *et al*. 1969; Tauzin 1994b; Luce 1996; Landvik 2000; Gusakov 2002; Zauli 2015). All members of the larger *Osmoderma* species complex have similar

habitus with pronounced sexual dimorphism, making gender identification possible in the field. Males have a shiny pronotum with two vertical ridges, while females have a matt-surfaced pronotum with lower ridges. Male individuals are also characterised by a vertically concave clypeus, making the head more angular (Tauzin 1994b; Gusakov 2002). Morphological differences between species in the *Osmoderma* complex are found in the male parameres, in the mesosternal plate of the abdomen, and on the elytral apex (cf. Baraud & Tauzin 1991; Sparacio 1993; Tauzin 1994b; Sparacio 2000; Gusakov 2002: Zauli *et al*. 2016). The species also differ in terms of DNA sequences from the mitochondrial *COI* gene, offering sufficient resolution to also distinguish between geographically separated populations (Audisio *et al*. 2009; Svensson *et al*. 2009; Zauli *et al*. 2016).

The larvae of the hermit beetle are typical, white scarabaeiforms (Fig. 1b) (Klausnitzer 1996), but potential morphological differences between the larvae of European *Osmoderma* species are currently unknown. In the last instar, the maximal length of the larvae reaches approximately 55–75 mm (e.g. Klausnitzer 1996). Cetoniinae species larvae have two moultings and three instars (e.g. Tauzin 1994b; Klausnitzer 1996). A lack of microsetae from the rear apex (see Klausnitzer 1996) separates the larvae of *Osmoderma* from other close relatives (e.g. *Protaetia lugubris*, *Cetonia aurata*, *Potosia cuprea*).

1.1.1   Taxonomy and distribution of European hermit beetles

The publication of the Habitats Directive of the European Union (Anonymous 1992) preceded the description of morphological differences between geographically separate populations (Sparacio 1993; Tauzin 1994a; Tauzin 1994b; Krell 1996; Gusakov 2002), and thus does not recognise any separate species of hermit beetles within Europe. The Catalogue of Palaearctic Coleoptera (Löbl & Smetana 2006) was thus the first systematic source to list European *Osmoderma* species as independent taxa. The genus name of *Osmoderma* was protected by the ICZN to avoid confusions in nomenclature (cf. Gusakov 2002; Smith 2004; ICZN 2007), and nowadays hermit beetle species are accepted as separate taxa also in Red Lists (e.g. Nieto & Alexander 2010; Carpaneto *et al*. 2015; Mauritzi *et al*. 2017). The latest updated nomenclature of *Osmoderma* has focused on geographical and genetic differences (Audisio *et al*. 2007, 2009).

The hermit beetle (*Osmoderma eremita* sensu lato) is separated into two clades and usually into four distinct species (cf. Löbl & Smetana 2006; Audisio *et al*. 2007, 2009; Mauritzi *et al*. 2017; Schoolmeesters 2017). The western clade occurs mostly from Central Europe westwards (e.g. north east Spain, France, Italy, Slovenia, western Germany, and Sweden, Denmark and Norway in Scandinavia). Populations of the eastern clade occur eastward of Central Europe (e.g. Croatia, eastern Germany, Greece, Poland, Slovakia) (Audisio *et al*. 2007, 2009; Svensson *et al*. 2009; Mauritzi *et al*. 2017). The

western clade comprises two accepted hermit beetle species (sensu stricto); *O. eremita*, and *O. cristinae* (Löbl & Smetana 2006; Audisio *et al*. 2007; Zauli *et al*. 2016; Mauritzi *et al*. 2017), whereas the species status of the South Italian taxon *O. italicum* remains uncertain. It is occasionally interpreted as a subspecies of *O. eremita* (see Audisio *et al*. 2007, 2009; Zauli *et al*. 2016), but sometimes accepted as a species (Löbl & Smetana 2006; Schoolmeesters 2017). The most widely distributed taxon is *Osmoderma eremita* s.s., which occurs in areas from Central Italy across Europe, reaching southern and central Sweden (cf. Ranius *et al*. 2005; Audisio *et al*. 2007).

The nomenclature and species status of the eastern clade *Osmoderma barnabita* and *Osmoderma lassallei* are still controversial (cf. Löbl & Smetana 2006; Audisio *et al*. 2007, 2009; Schoolmeesters 2017). The conflict originates from interpretation of taxonomical species names, as well as from modern methods of identification based on mitochondrial DNA (mtDNA). The accepted nomenclature has interpreted *O. lassallei* (occurrence in eastern Greece, and western Turkey) as a subspecies of *O. coriarium* syn. *O. barnabita* (Löbl & Smetana 2006; Schoolmeesters 2017), while mtDNA analysis based on the *COI* gene supports separate taxa (Audisio *et al*. 2009). Likewise, the IUCN Red List has evaluated *O. lassallei* as a separate taxon (Nieto & Alexander 2010). As mentioned above, the accepted nomenclature treats *O. barnabita* as a junior synonym for *O. coriarium* (Gusakov 2002; Löbl & Smetana 2006; Schoolmeesters 2017). However, the origin of the *O. coriarium* type specimen is from a Swedish collection (De Geer 1774), and is thus more likely to represent species *O. eremita* s.s. in the western clade (Audisio *et al*. 2007). For these reasons, I will be using the name *Osmoderma barnabita* Motschulsky, 1845, to refer to the widest-distributed taxon within the eastern clade of *Osmoderma* (Motschulsky 1845; Gusakov 2002).

1.2   The recent history of oak forests and the decline of saproxylic invertebrates

After the last glacial period, recolonisation of Northern Europe by deciduous forests started from refugia in more southern regions (Bennett *et al*. 1991; Taberlet *et al*. 1998; Hewitt 1999). Populations of pedunculate oak (*Quercus robur* L.) apparently survived in the Pyrenees, the Apennines, the Balkan Peninsula, and the Black Sea Lowland. They then expanded to their widest extent during the Atlantic period of the Holocene, 6000 BP (Taberlet 1998; Hewitt 1999; Brewer *et al*. 2002; Svenning *et al*. 2008; Stewart *et al*. 2010). In the north, the decline of the Baltic Sea level facilitated the colonisation of currently Finnish areas by oak-dependent taxa (Alho 1990; Jensen *et al*. 2002; Miettinen 2004). Nowadays, oaks in Finland mainly occur along the coastline (Lampinen & Lahti 2011), while during the climatic optimum of the Holocene, oak forests occurred much further to the north (Ferris *et al*. 1998; Donner 2005).

While the exact structure of post-glacial oak forests is still under scientific debate, the occurrence of closed oak forests seems unlikely (Kirby & Watkins 2016a). More probably, ancient oak forests were open, with a mosaic structure originating from large grazing mammals (Vera 2000; Mitchell 2005; Kirby & Watkins 2016a). Due to human influence, the range of European deciduous forests declined and was fragmented, as most forests were used as resources by humans (Williams 2006; Kirby & Watkins 2016b). Especially species requiring open landscapes benefitted from human actions, such as logging, firewood collecting, cattle grazing and urban park management (Nieto & Alexander 2010; Siitonen 2012c; Hartel *et al*. 2016). However, rapid changes in land use during the 20th century resulted in a decline of species inhabiting open woodland habitats. (cf. Nieto & Alexander 2010; Carpaneto *et al*. 2015; Westling 2015). In Finland, human influence is currently threatening organisms in the hemiboreal oak zone, which is already a very restricted forest type (European Environment Agency 2007; Rassi *et al*. 2010). Common causes for the decline of oak-dependent species are to be found in a decline in the availability of dead wood, and in forest succession in previously open landscapes (Nieto & Alexander 2010; Rassi *et al*. 2010).

1.2.1 Characteristics of saproxylic species

Broadly speaking, saproxylic species are organisms the life cycle of which depends on wounded or decaying wood (Speight 1989; Alexander 2008). In general, obligate saproxylics solely use microhabitats containing dead wood in their life cycle, while facultative saproxylics do not have to be strictly connected to dead wood resources (Stokland & Siitonen 2012b). Saproxylics can also be classified more accurately by their abilities to use microhabitats and by their dietary resources (see Bouget *et al*. 2005).

When the extent of old-growth broad-leaf forests has decreased, it has influenced the quality of forests, and the diversity of saproxylic species (Jonsson *et al*. 2005; Rassi *et al*. 2010; Jonsson & Siitonen 2012; Siitonen 2012b). The volume and quality of dead wood is reflected in the species richness of forests, with different saproxylics preferring different stages of the decay processes (Martikainen 2000; Lassauce *et al*. 2011; Stokland & Siitonen 2012a). The exploitable components of dead wood vary among different stages of decay, with variation in resources translating into variation in the diversity of saproxylic communities (Ehnström & Waldén 1986; Stokland & Siitonen 2012a). Saproxylic insects can utilise dead wood in many ways, but the primary energy sources are carbohydrates (cellulose) from recently dead trees or fallen branches (Szujecki 1987; Dajoz 2000; Stokland 2012a). On the other hand, saproxylics can also consume other organisms living in dead wood, e.g. fungal mycelium, plant structures, animals, or their faeces (Szujecki 1987; Farrell *et al*. 2001; De Fine Licht & Biedermann 2012; Stokland 2012b). Available nutrients may be scarce, especially at the end of the decay

processes, so saproxylic species have to obtain alternative sources, even by preying on other organisms (Ehnström & Waldén 1986; Stokland 2012b).

1.2.2 Saproxylic beetles (Coleoptera)

Well over half (66 %) of described animal species belongs to the class Insecta, wherein beetles (Coleoptera) are the most species rich order (Slipinski *et al*. 2011). The superradiation of beetle species has resulted in over 380 000 known species, and the actual number might be even bigger (Erwin 1982; Hunt *et al*. 2007; Bouchard *et al*. 2009; Slipinski *et al*. 2011). As a species rich taxa, saproxylic beetles offer high resolution in studies assessing the state of the environment (see e.g. Martikainen 2000; Lindhe 2004; Jansson 2009; Koch Widerberg 2013; Šebek 2016). In Europe, the estimated diversity of saproxylic beetles reaches perchance over 1000 to 4000 species, of which approximately 11 % are red-listed (cf. Stokland & Siitonen 2012b; Nieto & Alexander 2010; P. Audisio, Professor, Sapienza – Rome University, Italy, personal comment). However, almost one third (28 %) of beetle diversity is still in the category of data deficient (DD) taxa, so the number of threatened species may be bigger than so far estimated (Nieto & Alexander 2010). Among the red-listed beetles of Finland (333 species), decreasing availability of decaying wood has been listed as a cause of decline for 31 % of cases (Rassi *et al*. 2010).

Veteran trees are regarded as important hotspots for saproxylic beetle diversity – probably resulting from the wide variety of microhabitats in such trees (Speight 1989; Gough *et al*. 2014; Pilskog *et al*. 2016; Siitonen & Ranius 2016; Horák 2017). Many beetles can utilise recently dead branches (e.g. Cerambycidae, Curculionidae Scolytinae), others may live in fruiting bodies (e.g. Tenebrionidae, Staphylinidae), and some in tree cavities (e.g. Scarabaeidae Cetoniinae, Elateridae, Tenebrionidae) (Speight 1989; Bouget *et al*. 2005; Stokland 2012b). Tree hollows offer long-lasting habitat for many saproxylic species, providing resources for several decades, or even centuries (Ranius *et al*. 2009a; Manning *et al*. 2013). One key characteristic of such hollows is the formation of wood mould, promoted by combined effects of the cavicolous (i.e. hollow-inhabiting) community itself and of abiotic factors (Speight 1989; Ranius *et al*. 2009a; Siitonen 2012a; Siitonen & Ranius 2016). Accumulating wood mould can be composed of rotten wood from the cavity walls, fungal mycelium, plant-derived debris, animal faeces, and animal remains (M. Landvik, personal observations). Thus, a rich combination of wood mould components may also support diverse saproxylic communities, which usually consist of several threatened species (Ranius & Jansson 2000; Ranius 2002b; Jansson *et al*. 2009; Nieto & Alexander 2010; Carpaneto *et al*. 2015; Micó *et al*. 2015; Carlsson *et al*. 2016). Cavities are mainly confined to old trees, so the absence of veteran trees has a detrimental influence on cavicolous species diversity. A Swedish study has detected increased formation of hollows in trees over 200 years in age (Ranius *et al*. 2009a), and

there the hermit beetle (*Osmoderma eremita*) is mostly exploiting over 300 year old host trees (Ranius *et al*. 2009b).

1.3   The status of the hermit beetle in nature conservation

The hermit beetle is an umbrella species, and has been given the status of a priority species in the Habitats Directive of the European Union (Anonymous 1992; European Commission 2007). This status allows the conservation of larger communities dependent on veteran tree microhabitats (Ranius 2002a; Ranius 2002b). Saproxylic diversity is connected to sun-exposed woodlands in temperate forests (Ranius & Jansson 2000; Koch Widerberg *et al*. 2012; Gough *et al*. 2014; Seibold *et al*. 2014; Lachat *et al*. 2016). Additionally, the hermit beetle is known from a habitat identified as valuable for the conservation of saproxylic diversity in temperate forests (cf. Ranius & Nilsson 1997; Ranius *et al*. 2009b). The richest saproxylic diversity often occurs in the proximity of cultural habitats (Fig. 1c) such as open wood pastures, roadside trees, urban parks, hedgerows, small forest patches, or solitary veteran trees (Ranius & Nilsson 1997; Oleksa *et al*. 2007; Dubois *et al*. 2009; Vodka *et al*. 2009; Carpaneto *et al*. 2010; Chiari *et al*. 2012; Horák *et al*. 2014; Mauritzi *et al*. 2017).

The hermit beetle is also a hypothetical indicator of a rich diversity of invertebrates (Ranius 2002a). This indicator status may be rooted in the hermit beetle's ability to act as an ecosystem engineer: it is known that larvae are able to modify their microhabitat and thereby perhaps influence the diversity of other cavicolous species (Ranius 2002a; Jönsson *et al*. 2004; Chiari *et al*. 2014). Although nutrients decrease during the decay process, the larvae of hermit beetles (and other Scarabaeidae Cetoniinae) can enhance the level of nitrogen (N) and phosphorous (P) in their substrate (cf. Jönsson *et al*. 2004; Micó *et al*. 2011; Sánchez-Galván *et al*. 2014; Ulyshen 2016; Sánchez *et al*. 2017). In many cases, the growth of saproxylic juveniles depends on other organisms influencing the nutrient composition of dead wood (cf. Weslien *et al*. 2011; Filipiak & Weiner 2014; Ulyshen 2016), and thereby, the hermit beetle larvae may influence the surrounding cavicolous communities (cf. Sánchez-Galván *et al*. 2014).

1.4   Threats to saproxylics and to the hermit beetle

Human impact has diminished the original forest cover in Europe, with deforestation starting from the needs for fuel wood, charcoal production, shipbuilding and agriculture (Williams 2006; Kaplan *et al*. 2009; Büntgen *et al*. 2011). In the present day, the most important threats to saproxylics relate to forest logging, wood harvesting, and expansion of urban and agricultural areas (Nieto & Alexander 2010). As old growth deciduous

forests have shrunk, solitary veteran trees have become more important in urban areas, playing a key role as the last refugia for saproxylic organisms (Franc 1997; Flåten & Fjellberg 2008; Carpaneto *et al*. 2010). Unfortunately, aging trees are often seen as a threat to people, which can lead to tree removals before an older age is reached (cf. Jokinen 2017; Mäkinen 2017). Thus, the removal of veteran trees is a major threat to all saproxylics, as well as to hermit beetles (Nieto & Alexander 2010).

Forest dynamics have a big role in conservation, as lack of management can transform nature reserves into "hostile" environments wherein threatened species populations are struggling (Koch Widerberg 2013; Heikkala 2016; Šebek 2016). Therefore, the current trend in conservation is to include more management actions, and active interventions are becoming essential parts of conservation applications (Hunter 1993; Saint-Germain *et al*. 2004; Heikkala *et al*. 2014). The human influence has been exceptionally strong in temperate broadleaf forests, so termination of forest management may lead to detrimental outcomes for saproxylics (Franc & Götmark 2008; Vodka *et al*. 2009; Hédl *et al*. 2010; Koch Widerberg *et al*. 2012). Succession can be seen as one of the most harmful factors in temperate forests, wherein increased vegetation density often results in reduced biodiversity (e.g. Jonsell 2012; Paltto *et al*. 2011; Horák *et al*. 2014; Kirby & Watking 2016a; Sebek *et al*. 2016). Additionally, a closed forest structure in oak woodlands may eventually lead to the absence of forest regeneration, and increased mortality of old trees (Götmark 2007; Drobyshev *et al*. 2008). Thus, the minimal intervention approach, i.e. "hands-off" management, has been identified as a conservation strategy detrimental to supporting saproxylic species in temperate deciduous forests.

A decline in the species diversity of saproxylic taxa may lead to detrimental influences on secondary saproxylics. The hermit beetle is an example of a taxon which does not take part in early cavity formation, but enters later and requires wood mould in its hollow habitat (Speight 1989; Ranius 2007; Ranius *et al*. 2009b). Cavities can reach such a state after a long process, where first stage modifications are made by pioneer species followed by other species altering the cavity structure and the wood mould substrate (Siitonen 2012a; Siitonen & Ranius 2016). Many generalist saproxylics have rather flexible strategies for utilising dead wood, and likely play an important role in the colonisation of tree hollows (Speight 1989; Milberg *et al*. 2014). Those generalists may also have a keystone role in producing and modifying resources needed by later arriving species in tree cavity microhabitats. Currently, little is known about successional stages of tree hollows, and how species are influencing the quality of the wood mould. More studies are clearly needed to reveal the processes behind wood mould formation by cavicolous communities (see e.g. Jansson *et al*. 2009; Micó *et al*. 2015; Carlsson *et al*. 2016).

Small populations living in restricted locations are in danger of regional extinction (e.g. Ranius 2000; Ranius & Hedin 2004). The hermit beetle is regarded as a poor disperser,

which further increases the vulnerability of the species (Hedin 2003). Several studies have targeted the dispersal of the hermit beetle, with variable results in different geographical areas (Chiari *et al*. 2013; Oleksa *et al*. 2013; Valainis *et al*. 2015). Overall, as many as 85 % of individuals are assumed to stay in their natal trees (Ranius & Hedin 2001). In addition, hermit beetle dispersal and migration may also be prevented by a lack of optimal microhabitats, i.e. veteran tree cavities (Hedin *et al*. 2008). Inbreeding is one drawback for such stationary populations, leading normally to genetic erosion, and to low survival under sudden environmental changes (Frankham *et al*. 2009; Allendorf *et al*. 2013).

2.   AIMS OF THE THESIS

Over the last few decades, the hermit beetle, *Osmoderma eremita* sensu lato, has been the topic of intensive research. These studies have increased our knowledge regarding its taxonomy, habitat requirements, population dynamics, dispersal abilities, and response to semiochemicals. However, different studies have yielded somewhat different results, perhaps partly resulting from variation in the methodology used, from impacts of the surrounding communities on the focal species, and/or from differences in the ecology of different cryptic species within the *Osmoderma* species complex. In addition, organisms are always influenced by their genetic composition, and therefore behavioural patterns may differ among individuals from the same area, and even more among individuals from different regions (cf. Ranius & Nilsson 1997; Hedin *et al*. 2008; Chiari *et al*. 2012; Chiari *et al*. 2013). In Finland, the hermit beetle reaches its northern range margin, and here the climate and the vegetation will clearly differ from that of areas in the southern part of the species' distribution (Metzger *et al*. 2005; Ranius *et al*. 2005; European Environment Agency 2007). Thus, there is a possibility that study results from other regions are not applicable to the Finnish population, and that conservation guidelines derived elsewhere may not promote the conservation and management of the species in Finland (cf. Ranius & Nilsson 1997, Landvik 2000; Oleksa *et al*. 2007; Ranius *et al*. 2009b; Chiari *et al*. 2012). Moreover, the taxonomy of the Finnish population had never been studied, so even its exact species affinity remained unknown (cf. Ranius *et al*. 2005; Audisio *et al*. 2007, 2009). Thus, the primary aim of the current thesis is to explore the identity, ecology and conservation of the northernmost occurrence of the hermit beetle in Finland. More specifically, I ask:

1)   *Which cryptic Osmoderma species occurs in Finland?* The latest red-listing of Finnish species (Rassi *et al*. 2010) evaluated the hermit beetle as belonging to *Osmoderma eremita* (Scopoli, 1763) within the western clade, but the species hypotheses of Audisio *et al*. (2007, 2009) suggest that the Finnish population may belong to *Osmoderma barnabita* Motschulsky, 1845, within the eastern clade.

2)   *What is the history of the Finnish the hermit beetle population?* Presumably, the post-glacial migration has influenced the structure of subpopulations (see Hewitt 1996, 1999; Audisio *et al*. 2009).

3)   *Is the Finnish occurrence of the hermit beetle really restricted only to the Turku region?* The tentative map of the IUCN (cf. Alexander *et al*. 2010) – based on the distribution of its presumed habitat – proposes a much larger range for the hermit beetle in southern Finland than previously observed.

4)   *What are the habitat requirements of the hermit beetle in Finland?* Previous studies suggest that hermit beetles require large-sized hollow trees, cavities containing abundant wood mould, and trees located in open environments (e.g. Ranius & Nilsson 1997; Ranius *et al*. 2009b).

5)   *How does the chemical quality of wood mould affect larval growth and female oviposition?* A wide body of literature suggests that insect females favour resources optimal for larval development (Gripenberg *et al*. 2010). Based on substantial quantities of wood mould in cavities preferred by the hermit beetles (e.g. Hedin 2003; Ranius 2007; Ranius *et al*. 2009b), it may be hypothesised that wood mould is both beneficial to larval development and preferred by ovipositing females.

3.   MATERIAL AND METHODS

3.1   Study sites

For this doctoral thesis, I studied sites located in old cultural environments, where human influence has modified the landscapes. The main data of publications (**I-IV**) have been collected from southwest Finland, in the Turku region (8.3 km²) (Fig. 2). The coordinates of specimens sampled are provided in appendices of the individual publications. The reference material used in publication **II** was mostly collected from the northern Pededze Valley, Latvia (Fig. 2), where samples were obtained from small oak patches and roadside trees in northern Lubāns (4.1 km²). The collection sites of single specimens from Eastern Europe are presented in publication **II** (map), with accurate coordinates offered in the Appendix of the same paper (see **II** Appendix). Data on the distribution of *Osmoderma* (**III**) were obtained by volunteers sampling across southern Finland (see **III** Appendix S1, A, Text 1), whereas data on local occupancy and habitat requirements (**III**) were collected on the island of Ruissalo. Similarly, all individuals measured and observed in paper **IV** originated from Ruissalo.

Fig. 2. The location of the main study sites. All main datasets (I–IV) were obtained in Finland, Turku Ruissalo Island 60°26´N 22°11´E, with complementary data for paper II gained in particular from Latvia, Pededze Valley 57°04´N 26°53´E. The coordinates are given in WGS 84.

The main study site, Ruissalo Island (total area 9 km²), covers the largest and maybe the most significant oak population within the Finnish oak zone (Vuorela 2001; Rassi *et al*. 2010). The vegetation of the island has been influenced by humans for centuries, but a recent strategy of minimum intervention has made the structure of the forests denser and more closed (Vuorela 2001). However, the island is still very diverse, encompassing oak forests, small forest patches, semi-urban parks, roadside alley trees, private gardens, small meadows, crop fields, and a golf course with solitary trees (Vuorela 2001; Anonymous 2006). The herb-rich forests and small oak patches are protected as nature reserves, or belong to the Natura 2000 network (Anonymous 2006). Nevertheless, a significant number

of veteran trees are located in public parks, private yards, on roadsides, and on a golf course (Eerikäinen *et al*. 2010). Extended information on history, vegetation, and human influence in Ruissalo is provided in paper **III** (**III** Appendix S1, Text 2).

3.2   Biology and ecology of the study species

The life cycle of the *Osmoderma* species complex is connected to old, large-sized veteran trees in open landscapes (Ranius *et al*. 2005). As the optimal microhabitat, Ranius *et al*. (2009b) identify a hollow oak tree with a large volume of wood mould in its large cavity. However, geographical variation in the species' habitat characteristics is known, and the hermit beetle has been observed from over 20 host tree species (Ranius *et al*. 2005). In Sweden, the main host is *Quercus robur* (Palm 1959; Ranius & Nilsson 1997), in France the main hosts are *Quercus robur* and *Malus domestica* (Dubois *et al*. 2009), in Italy the southern oak species *Quercus* sp. (Chiari *et al*. 2012; Mazzei *et al*. 2014; Mauritzi *et al*. 2017), and in Poland *Tilia cordata* and several other species (Oleksa *et al*. 2007; Kadej *et al*. 2016). Cryptic *Osmoderma* species may have different habitat requirements (Siitonen & Ranius 2016), or alternatively be constrained by variation in the longevity of hollow habitats (cf. Ranius *et al*. 2009a).

Communication among the hermit beetle populations occurs mainly via pheromone (*R*)-(+)-γ-decalactone (Larsson *et al*. 2003), which seems to be similar among all European *Osmoderma* species (Svensson *et al*. 2009; Zauli *et al*. 2016). Males emit the airborne pheromone, attracting other individuals to disperse, and females to mate in hollow tree sites (Larsson *et al*. 2003; Larsson & Svensson 2009; Larsson & Svensson 2011; Svensson *et al*. 2011). The disperal rate of *O. eremita* s.s. in the western clade seems to be rather poor, and most individuals reach very short distances (Ranius & Hedin 2001; Hedin & Ranius 2002). Evidently the majority stay in their natal tree, and only few individuals fly over distances of more than a kilometre (Hedin *et al*. 2008; Dubois *et al*. 2010; Chiari *et al*. 2013). The western clade of *Osmoderma* is also assumed to have adapted to the local climate, and individuals in the Mediterranean region may be able to reach longer dispersal distances (Ranius *et al*. 2005; Chiari *et al*. 2013). Likewise, species *O. barnabita* s.s. in the eastern clade may have the capacity for maximal flight distance of over two kilometres (Valainis *et al*. 2015). Yet, the dispersal of *O. barnabita* seems to be mostly based on short flights (Oleksa *et al*. 2013; Valainis *et al*. 2015). Overall, the dispersal abilities seem rather similar among all *Osmoderma* species, and slight variation in the results of individual studies may be attributed to methods, study areas, or climate.

The fecundity of hermit beetles has been observed to be rather low (Jönsson 2003; Tauzin 2005; Svensson *et al*. 2011), but can be promoted by several ovulations among longer-lived individuals (Luce 1995; Dubois 2009). Mated females lay their eggs (1-25) into the wood

mould of hollow trees, where they hatch after two to three weeks (Tauzin 2005; Svensson *et al*. 2011). Larvae hatch from swollen, enlarged eggs, and their growth is solely restricted to the cavity habitats (Luce 1995; Ranius *et al*. 2005; Dubois 2009). Larvae of the hermit beetle are considered to feed on several dietary resources, but primarily on dead wood (Dubois 2009). In such habitat they may feed on the cavity walls themselves (Ranius *et al*. 2005; Siitonen 2012a), on the mycelium covered walls (Luce 1996), on wood mould or on wood at all stages of decay (Carpaneto *et al*. 2015). Growing larvae undergo two moulting and hibernation stages before pupation, but the overall larval cycle ranges from two to six years (Ranius *et al*. 2005; Dubois 2009). Observations suggest that population performance is affected by the cavity material, with large volumes of wood mould enhancing the survival of populations, and increasing the size of adult individuals (Hedin & Mellbrand 2003; Hedin & Smith 2003; Ranius 2007; Ranius *et al*. 2009b). Moreover, *Osmoderma* larvae modify the chemical quality of the wood mould by releasing more nitrogen (N) and phosphorous (P) to the substrate (Jönsson *et al*. 2004). The origin of these increased nutrient contents are assumed to relate to nitrogen-fixing gut bacteria, the actual presence of which has not yet been proven (Jönsson *et al*. 2004). Similarly, observations from other rose chafer species indicate a capacity of *Cetoniinae* larvae to influence the nutrient composition of their substrate (e.g. Li *et al*. 2006; Micó *et al*. 2011; Sánchez-Galván *et al*. 2014).

After the final hibernation, *Osmoderma* larvae use compounds from wood mould to construct a cocoon (syn. coccolith), which protects the pupal stage and the newly hatched adult beetles (Szujecki 1987; Tauzin 1994b; Tauzin 2005). Upon hatching, the imago stays in its cocoon for several weeks, awaiting the hardening of its chitin exoskeleton (M. Landvik, personal obervations). The adult beetles emerge from late June to late July in the northern hemisphere, but the weather can influence the emergence and activity of individuals (Landvik 2000; Ranius *et al*. 2005; Oleksa & Gawronski 2008). As an adult, the hermit beetle has been observed to feed on tree sap, and even on flowers (Ranius *et al*. 2005). Yet, due to limited dispersal capacity, individuals may not normally waste their energy resources on foraging (cf. Hedin *et al*. 2008; Klowden 2013). The life expectancy of males is approximately one week in Scandinavia, while females are able to live for a month under natural conditions (Ranius *et al*. 2005).

3.3   Mitochondrial *COI* variation

Maternal mtDNA-genotypes form matrilinear groups (haplotypes) among animal species, which can be used in phylogenetic analysis and phylogeography (Avise 2004; Frankham *et al*. 2009). Generally, the use of mtDNA in animal taxonomy is currently focused on the identification of cryptic species (e.g. Hebert *et al*. 2004; Murray *et al*. 2008; Pentinsaari *et al*. 2014b; Fennessy *et al*. 2016). In population genetics, it can reveal the species' genetic demographic history (e.g. Beheregaray *et al*. 2003; Todisco *et al*. 2010; Moodley *et al*. 2017).

A DNA barcode is a 658-basepair (bp) sequence of the mtDNA *COI* gene, which can be exploited especially in macroevolutionary studies (Hebert *et al*. 2003; Ratnasingham & Hebert 2007; Valentini *et al*. 2009; Hebert *et al*. 2016). Normally, speciation produces a clear increase in sequence divergence (a so-called barcode gap between species), whereas intraspecific diversity is typically confined to more closely related haplotype groups (e.g. Hebert *et al*. 2004; Jackson *et al*. 2014; Ashfaq *et al*. 2015). Barcode-based identification will typicaly provide reliable species identification (e.g. Hajibabaei *et al*. 2006; Williams *et al*. 2006; Audisio *et al*. 2009; Svensson *et al*. 2009; see Pentinsaari *et al*. 2014a, 2016 for patterns among beetles). Generally, the *COI* marker is very useful with sibling and cryptic species, the morphological characteristics of which may be either arbitrary or non-existent (e.g. Woodcock *et al*. 2007; Huemer *et al*. 2014; Clayhills *et al*. 2016).

DNA sequence variation will also offer insights into the demographic history of populations (Avise 2000, 2004; Frankham *et al*. 2009). Such knowledge is a key element in species protection, as it offers the delineation of revelant target units for conservation (cf. Abellán *et al*. 2007; Gratton *et al*. 2008; Frankham *et al*. 2009; Todisco *et al*. 2010; Allendorf *et al*. 2013). Due to insufficient repairing mechanisms of the mitochondrion (compared to nuclear DNA), the *COI* gene has a high resolution in demographic analyses of the Quaternary (Avise 2004; Fahey *et al*. 2014). Thus, *COI* is an effective gene marker to reveal historical events of a population, such as bottlenecks and founder effects (e.g. Ashfaq *et al*. 2015; Collins & Hogg 2016; Lasota *et al*. 2016; Mestre *et al*. 2016). For studies requiring high resolution, nuclear DNA markers (or microsatellites) are typically used to either substitute or complement insights gained with *COI* (e.g. Solano *et al*. 2013; Drag *et al*. 2015; Costion *et al*. 2016).

3.4   Study material

The field data for this doctoral study were collected during 2010–2014, mainly from June to August. Exact timings are presented in study papers (**I**, **II**, **III**, **IV**). Some samples and specimens were obtained from an open access database (GenBank), and natural history museums (**I**, **II**). The oviposition study, and the larval rearings (**IV**) were performed after the field seasons of 2012–2014. The chapters below briefly review the methodology of the data used in the thesis papers (**I**–**IV**).

3.4.1   Pheromone trapping (I – IV)

Material on adult beetles (**I**–**IV**) was mainly collected by pheromone trapping (Fig. 3). In publications **I** and **II**, DNA fragments were obtained from pheromone trapped beetles, which were released after sampling. The distribution study (**III**) was based on pheromone trapping across southern Finland. In publication **IV**, females for the "cafeteria experiment"

Fig. 3. Samples in Finland and Latvia (I-IV) were collected by using a trunk-touching pheromone trap, a new design invented in 2010 for this thesis work (Landvik *et al*. 2015). The trunk-touching trap does not require beetles to fly and hit any trap structures, as the commonly-used black cross window model does. Rather, the trunk-touching trap model targets the normal behavior of *Osmoderma* sp. walking on the tree trunk, permitting beetles to enter the trap freely. The main components of the trap are: (i) an ear for uplifting; (ii) a funnel (18 cm upper diameter) cut from the front edge; (iii) a collecting container (500 ml) with humus; (iv) a string for placing and fastening the trap on tree; (v) a cotton roll for the pheromone, placed with a holder into the funnel neck; and (vi) small holes for releasing rain water from the container. Photographs © Matti Landvik.

and oviposition trials were collected with pheromone traps. Pheromone trapping was based on a racemic mixture of +-γ-decalactone, as it has proved to be a powerful method in monitoring diverged hermit beetle species in Europe (Svensson *et al*. 2009).

3.4.2   DNA samples (I, II)

For revealing the taxonomical status of the Finnish hermit beetle (**I**), sample specimens were collected by pheromone trapping (Fig. 3). Mitochondrial DNA *COI* analysis was performed after DNA extraction from leg samples, polymerase chain reaction (PCR), and sequencing. The Finnish sequences (approx. 1 400 bp) were combined with previously published data by Audisio *et al*. (2009) and Svensson *et al*. (2009), with a total dataset of 45 sequences. All Finnish sequences included shortages in the first bases of the *COI* gene (KC476172-KC476178), which prevented the use of these samples in the following paper (see paper **II**). The Finnish *Osmoderma* species status from mtDNA *COI* sequences was analysed using MrBayes 3.1 (Ronquist & Huelsenbeck 2003), and evolutionary distances between and within groups were calculated in MEGA5 (Tamura *et al*. 2011). See detailed methods in publication **I**.

Demographic history and phylogeographic substructuring of the East European hermit beetle populations (**II**) were studied from newly gained *COI* gene sequences (*n*= 193)

Fig. 4. Wood mould sampling in narrow and deep cavities was performed with a battery-operated vacuum cleaner (III). A series of narrow tubes (originally electrical conduits) enhanced sampling from small entrance holes when the wood mould surface lay several metres below the entrance hole. Photograph © Matti Landvik.

and previously published data (Audisio *et al*. 2009). All *COI* sequences in the final dataset (*n*= 196; see **II** Appendix 1) were edited to the length of 759 base pairs. Genetic diversity was analysed and estimated by separating the dataset into three geographical regions: (i) Baltic region including West Russia; (ii) Central and Eastern Europe; and (iii) southwestern Finland. Mitochondrial *COI* diversity was estimated from haplotype number (*hn*), haplotype diversity (*h*), mean pairwise difference of nucleotides (*ī*), and nucleotide diversity (π). The total dataset was analysed under demographic models: (i) a constant population size model, (ii) a sudden demographic expansion model, and (iii) a spatial demographic expansion model. The sum of the squared deviations (*SDD*) and Harpending's raggedness index (*hg*) (Rogers & Harpending 1992; Harpending 1994) were used for analysing significance of differences between observed and simulated expected distributions. Additionally, the post-glacial expansion of *O. barnabita* was also analysed by using neutrality tests (Tajima 1989; Fu 1997; Ramos-Onsis & Rozas 2002), and by comparing haplotype diversity (*h*) and nucleotide diversity (π). All statistics and the constant population size model were run and calculated in DnaSP ver. 5 (Librado & Rozas 2009), and the expansion models in Arlequin ver. 3.5 (Excoffier & Lischer 2010). See detailed methods in publication **II**.

3.4.3 Occupancy sampling (III)

To obtain distribution data from the south coast of Finland (**III**), I aimed to sample the hypothetical range outlined in the IUCN Red List Data (cf. Alexander *et al*. 2010). During the study years 2012–2014, a citizen science based survey was performed (21 persons) across 52 sites by using "trunk-touching" pheromone traps (*n*= 112), which were placed

on optimal habitats (Fig. 3). Monitoring was conducted during the main flight period of the hermit beetle in Finland (Landvik 2000). Details of the distribution study are provided in paper **III** (**III** Appendix S1, A, Text 1).

3.4.4 Habitat characterisation (III)

The study of habitat requirements of *Osmoderma* (**III**) was focused on the main area of occupancy in Finland (Turku, Ruissalo Island). Study was performed by sampling wood mould of hollow trees and their nearby environment, before the main emergence season of *Osmoderma* adults. A vacuum cleaner was used in deep cavities when a small or narrow entrance hole complicated sampling (Fig. 4). The method allowed sampling from narrow (diameter <10 cm) cavities with a depth of over three metres. The presence of *Osmoderma* in hollow trees was recorded by identifying larval faecal pellets (see Szujecki 1987), and chitin fragments of adult beetles (cf. Tauzin 1994b; Gusakov 2002). Habitat characteristics were analysed by using descriptors of the hollow microhabitat, the tree individuals, the insolation, and the accessibility (see **III** Appendix C, S3, Table C1). Statistical analyses were performed in SAS Systems v. 9.4 for Windows, proc Genmod (SAS Institute Inc., Cary, NC, USA). Details of the sampling methods and statistical analyses are provided in publication **III** (**III** Appendixes S1-S4, A-D).

3.4.5 Experiments on larval diet and female oviposition (IV)

The habitat use study of the hermit beetle (**IV**) was divided in to three parts, addressing (respectively); (i) the influence of wood mould quality on larval growth and mortality, (ii) the influence of microbes on larval growth and mortality, and (iii) the preference of ovipositing females for specific substrates. Studies were performed in three seasons 2012–2014. Data from the larval rearing experiment, microbial experiment, and female preference experiment were analysed with SAS for Windows ver. 9.4, proc Glimmix (SAS Institute Inc., Cary, NC, USA). The main methods are summarised below, with details provided in paper **IV**.

To reveal the influence of wood mould quality on larval growth and mortality, larvae were reared on rotten oak wood (brown-rot wood), hermit beetle faecal pellets (larval frass), and decaying broadleaves (leaf humus) (cf. Fig. 5a; **IV** Fig. 1). Generally, selections were based on observations in study **III**: (a) the most common substance in cavity walls (brown-rot wood); (b) a compound present in every hermit beetle cavity (the species' own frass); and (c) random plant-derived subsidies entering the cavity from outside (leaf humus). Pedunculate oak (*Quercus robur*) was observed to be the main host tree in the Finnish area of occupancy (cf. **III**), with cavity surfaces mainly covered by brown-rot wood (Speight 1989). A large quantity of brown-rot wood originates from the cavity formation process of *Laetiporus sulphureus* (Stokland *et al*. 2012), which is commonly seen in oak
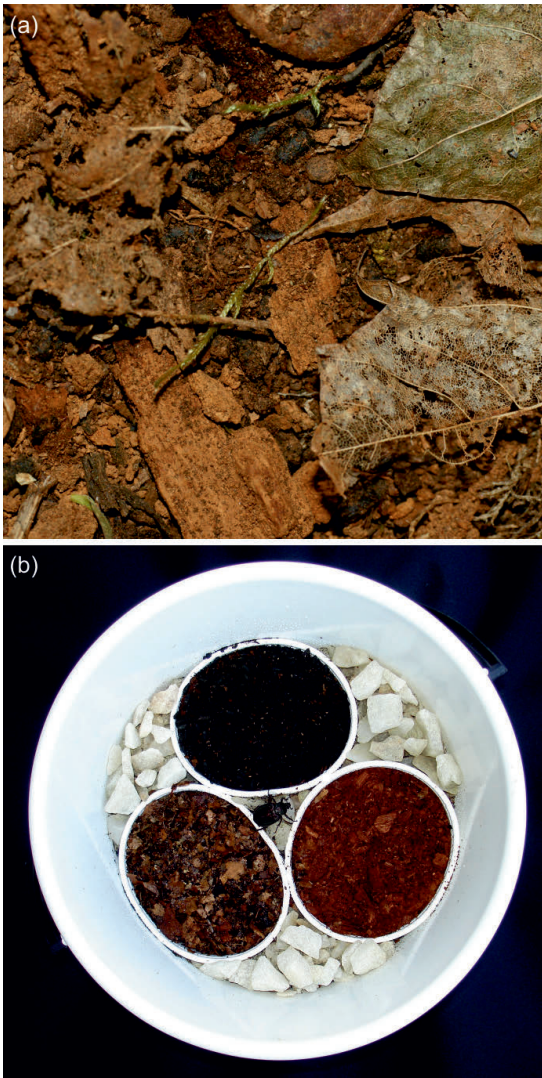
Fig. 5. The common substances of wood mould in Finnish hollow trees (a) were observed to comprise mainly brown-rot wood (decaying oak wood), larval frass (*Osmoderma* faecal pellets), and plant-derived decaying material (e.g. leaf humus). These same components were used as the main substrates in the larval rearings and in the female preference test (IV). In the preference test (b) all females were placed in a "cafeteria experiment" with free access to choose the substrate (brown-rot wood, frass, leaf humus) for egg-laying. Photographs © Matti Landvik.

hollows of Ruissalo (M. Landvik, personal observations). The hermit beetle larval frass (faecal pellets) was chosen for a substrate component due to stationary populations, as host trees cavities can contain several litres of the species' own excrements (Ranius *et al*. 2005; Ranius *et al*. 2009a). Leaf humus was chosen as a third main component of wood mould substrates, here presenting one possible material of subsidies entering from outside the cavity. Leaves can float randomly into small and larger holes, unlike many other plant structures which may need facilitated diffusion to reach the wood mould surface (e.g. moss, bigger tree brances). Twelve treatments were formed using the main substrates (similar to **IV**, Fig. 1), and 308 larvae were reared in two study periods. The three-month study period was assumed to correspond to optimal larval development during the first growth season in the Finnish environment. See detailed larval rearing methods in publication **IV**. The quantities of different elements in the main substrates

were also analysed by ICP-OES, following methods by Seleiman *et al.* (2012) (see details in **IV** ESM1).

To reveal the microbial influence on larval growth and mortality, individuals were reared in normal unsterilised frass (*n*= 20), sterilised frass (*n*= 20), and fungal mycelium (*n*= 15). Larval frass contains concentrated elements (N, P), potentially promoting larval growth of cavicolous species, thus also influencing *Osmoderma* larval growth (cf. Jönsson *et al.* 2004; Sánchez-Galván *et al.* 2014). As Luce (1996) assumed hermit beetle larval to exploit mycelium covered cavity walls, *Laetiporus sulphureus* was tested with a group of larvae, using small chips of mycelium. All individuals (*n*= 55) in the above mentioned three groups were incubated in unsterilised frass, and neonate larvae were placed in individual containers with a specific study substrate. All other procedures were similar to the larval rearing experiments (**IV**) above, except the length of the study period, which was prolonged to four months (25 August – 22 December 2014). This extension of the study period allowed better possibilities for measuring and observing larval preparation for diapause. See detailed microbial experiment methods in publication **IV**.

To reveal oviposition preference I designed a "cafeteria experiment", wherein a hermit beetle female was able to choose its egg-laying site between all main substrates presented simultaneously (**IV**). Females (*n*= 34) were placed in separate 10 litre buckets, each with three smaller containers of the main substrate (brown-rot wood, larval frass, and leaf humus), with coarse dolomite on the surface between containers (Fig. 5b). Female choice was scored after the study period (4 August – 29 September 2014) by counting all eggs and larvae. See detailed female preference experiment methods in publication **IV**.

4.   MAIN RESULTS

4.1   Taxonomy of the Finnish hermit beetle population (I)

Mitochondrial *COI* sequences from the Finnish hermit beetle population are more closely related to East European *Osmoderma barnabita* populations than to any other European *Osmoderma* species. The low level of sequence divergence (0.6 %) between Finnish specimens and *O. barnabita* sequences on average suggests that they are indeed conspecific with East European *O. barnabita* populations. Among Finnish specimens, divergence was minimal (0.1 %), with all belonging to two closely related haplotypes in sequences of ca. 1400 base pairs. The *Osmoderma* species next-most similar to the Finnish sequences was Greek *O. lassallei*, which has previously been identified as a member of the eastern clade of hermit beetles (Audisio *et al*. 2007; 2009). However, interspecific sequence divergence (10.6 %) between *O. barnabita* and *O. eremita* suggests long-term separation between the two taxa, with the level of divergence being close to the average value among separate beetle (Coleoptera) species (Pentinsaari *et al*. 2014a).

The current results support the hypothesis advanced by Audisio *et al*. (2007; 2009), suggesting that *O. barnabita* is widely distributed across Eastern Europe. From a Finnish perspective, Swedish hermit beetle populations are relatively close in space (less than 300 kilometers from Ruissalo), but represent a different species (Ranius *et al*. 2005; Audisio *et al*. 2009; Svensson *et al*. 2009). Thus, information derived from Sweden, or from other parts of the range of the western clade (e.g. France, Italy), should not uncritically be assumed to apply to Finnish *O. barnabita* (e.g. Ranius & Nilsson 1997; Dubois *et al*. 2009; Chiari *et al*. 2012), as separate species may differ in their ecology and habitat use (Siitonen & Ranius 2016).

In current taxonomical nomenclature, *O. barnabita* has been regarded as junior synonym for *O. coriarium* (cf. Gusakov 2002; Löbl & Smetana 2006; Schoolmeesters 2017). However, the latter type specimen (*Scarabaeus coriarius*, De Geer 1774) has not been exmined for diagnostic morphological characters (Gusakov 2002), was collected from an unknown locality (De Geer 1774) and offers no possibilities for DNA analysis (J. Bergsten, Senior curator, Swedish Museum of Natural History, Stockholm, personal comment). Instead, the type specimen of *O. barnabita*, originally named by Victor de Motschulsky (1845), has been analysed and identified as representing the hermit beetle species present in large parts of Eastern Europe (cf. Gusakov 2002; Audisio *et al*. 2007, 2009). Due to these inadequacies (see De Geer 1774; Gusakov 2002), the name *Osmoderma barnabita* Motschulsky, 1845 should be adopted when referring to the Finnish hermit beetle species.

4.2   Demographic history and subpopulation structure of the hermit beetle in Eastern Europe (II)

The mtDNA *COI* haplotypes (in 759 bp sequence) were non-overlapping among regional populations of *O. barnabita*, establishing separate geographical groups in different parts of Europe. All haplotypes (*n*= 26) were closely related to each other and separated from the central haplotype occurring in the Baltics (HT5) by only one to four mutations. However, due to low sampling in southern regions, several other central haplotypes might have gone undetected, and *O. barnabita* may exhibit richer genetic diversity than here estimated. Nonetheless, a star-shaped topology of the haplotype network is characteristic of population expansion after a bottleneck (Fig. 6), wherein mutations form groups from the central haplotype (e.g. Avise 2000; Fahey *et al*. 2014). Regionally separated subpopulations with diverged haplotypes suggest a mechanism increasing sub-structuring, wherein current gene flow is too weak to homogenise genetic composition.

All diversity indices of *COI* gene (*h*, *ī*, π) decrease northwards indicating post-glacial migration from a more diverse southern origin. Tests to resolve demographic history (Tajima *D*= -1.9575, *p*= 0.002; Fu *Fs*= -22.2775, *p*= 0.000) suggested either an expansion or a strong selection within the overall population of *O. barnabita* in East Europe. Expansion of total population was further confirmed by significant values of Ramos-Onsins' and Rozas' statistic (R_2= 0.0257, *p*= 0.029), which is able to detect expansions from a small sample size. Harpending's raggedness (*hg*= 0.0275, *p*= 0.025) rejects H_0 of constant population size, implying that post-glacial expansion has occurred among the total population of *O. barnabita*. Also, two final models of demographic expansion could not be rejected (sudden demographic expansion *versus* spatial expansion model), and thus patterns seem compatible with all models. Overall, statistical analyses further support post-glacial expansion northwards from the Balkan Peninsula, or from some (currently unknown) cryptic refugia (cf. Hewitt 1996, 2004; Stewart & Lister 2001; Audisio *et al*. 2009; Schmitt & Varga 2012).

The *COI* haplotype of the Finnish population (HT4; 759 bp sequence) differs only by one mutation from the central haplotype of the Baltic region (HT5), likely founding the genetic stem to northern populations. The Finnish hermit beetle haplotype was also found to be unique in Europe, being entirely monomorphic in its area of occupancy. The lack of variation may originate from the events of recent demographic history, wherein founder effect, and/or bottleneck effect has narrowed the genetic diversity of the Finnish population. When comparing *COI* haplotype number and diversity between the Turku region (a sampling area of approx. 8.3 km²) and Pededze Valley in Latvia (a sampling area of approx. 4.1 km²), it is easy to notice the distinct difference between these two neighbouring areas (Fig. 6). This indicates that the Finnish region was the last region to be colonised during the European post-glacial expansion. Yet, the current results fail to establish the exact colonisation route to Finland, with two options being (i) migration
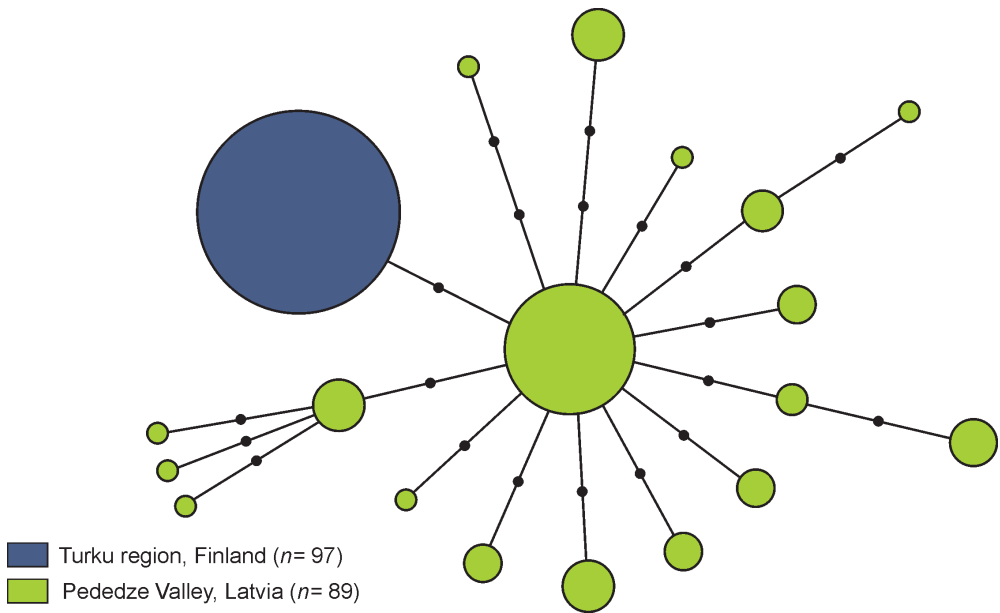
Fig. 6. Historical events have influenced the genetic structuring of Finnish (Turku region) and Latvian (Pededze Valley) populations (II). Both populations show signs indicating a strong selection or bottleneck, which appears to have occurred more recently or strongly in Finland. The Latvian population has also derived a wide number of separate haplotypes from its central haplotype. The size of the circle represents the number of individuals exhibiting each mitochondrial *COI* haplotype (759 bp sequence). The size of the sampling area was 8.3 km² in the Turku region and 4.1 km² in Pededze Valley. (Reproduced and modified from Landvik *et al*. 2017. Nature Conservation 19:171-189 doi 10.3897/natureconservation.19.12877; see original article II).

from east through the Karelian Isthmus, and across coastal areas, and/or (ii) a passage across the Gulf of Finland from the Baltic region (cf. Ferris *et al*. 1998).

Future studies would require a wider sampling area, bigger dataset, and more comprehensive genetic markers for revealing the more presice delimitation of *O. barnabita* subpopulations in Eastern Europe. For the conservation of the hermit beetle in Finland it is important to ascertain if *COI* monomorphisms also reflect more general reduced genetic variability. Importantly, mtDA is more sensitive to bottleneck effects than nuclear genes, given a smaller by half effective population size (being maternally inherited; Avise 2004). Genetic impoverishment may cause further threat if new invasive species, pathogens, or environmental change affect the Finnish population (cf. Frankham *et al*. 2009; Allendorf *et al*. 2013).

4.3   The distribution and habitat of the hermit beetle in Finland (III)

4.3.1 Distribution (III)

The hypothetical distribution map presented by the IUCN (see Alexander *et al*. 2010) failed to gain any support from our large-scale empirical sampling. In total, 21 persons
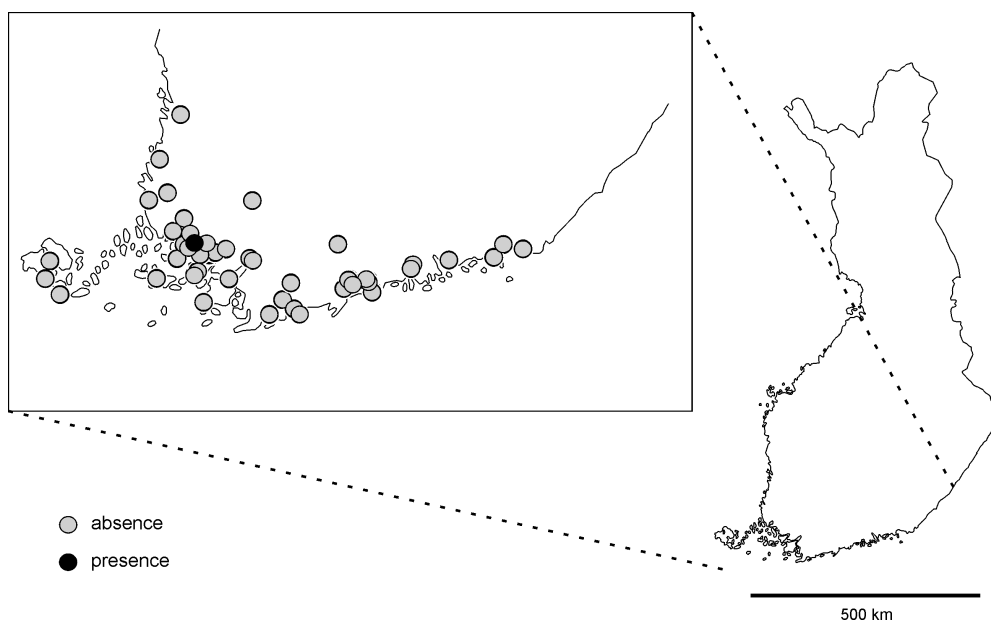
Fig. 7. Extensive sampling by pheromone traps (2012-2014) established the Turku region as the only occurrence of the hermit beetle in Finland (III). Some specimens detected in Raisio (Huhko) were found at a distance of only four kilometres from Ruissalo Island in the Turku region. (Reproduced and modified from Landvik *et al*. 2016. Insect Conservation and Diversity 9 (1):38–48 doi 10.1111/icad.12141; see original article III).

sampled the full proposed range using a total of 112 pheromone traps across 52 study sites (see **III**, Appendix S1, A, Text 1). The only findings were made within 4 kilometers from Ruissalo Island, on a site (Raisio, Huhko) in the Turku region (Fig. 7). This collecting site did not reveal any signs of *Osmoderma* larvae, so the two imagos caught may have originated from Turku. More specifically, these two females may have flown from hollow trees outside of Ruissalo Island (Artukainen, Perno) previously established as occupied by *Osmoderma* in inventories of the Turku city area (M. Landvik, unpublished data). The lack of any findings outside of the Turku region suggests a true absence of other viable hermit beetle populations anywhere in Finland. Moreover, the results imply that Ruissalo may be the only Finnish oak stand large, old and continuous enough to sustain a viable metapopulation of *O. barnabita* in South Finland (cf. Valtakunnallinen lehtojensuojeluohjelma 1989; Ranius 2000; Hedin 2003; Ranius & Hedin 2004).

4.3.2 Habitat (III)

Of the total of 192 hollow trees examined, 62 trees (i.e. 32 % of the trees sampled) showed signs of *O. barnabita*. Chitin fragments alone were found in 4 trees, while larval frass was found in a total of 58 trees scored as occupied, 33 of which contained both frass and chitin fragments. The most abundant hollow tree species was pedunculate

oak (*Quercus robur*) with 75 studied trees, among which signs of beetle presence were encountered in 50 oaks (67 %). Incidence in lime trees (i.e. *Tilia* x *vulgaris*, *Tilia cordata*) was also rather high (*n*= 7 finds among 33 hollow limes examined; 21 %). In alders (*Alnus glutinosa*), incidence was clearly lower, with larval frass detected in only two (6 %) of 32 hollows inspected. Single signs of *Osmoderma* presence were also detected in the taxa *Acer platanoides*, *Sorbus aucuparia*, and *Populus nigra*, so conservation management should not rule out *Osmoderma* occurrence among other tree species on Ruissalo Island.

Statistical analyses identified tree species (*Quercus robur*) and tree size (large diameter) as the strongest factors impacting *Osmoderma* incidence (Fig. 8). The same factors were selected as significant for both larval frass and adult chitin fragments, despite the fact that occupancy for a whole of 27 cavities was scored differently when using the respective indicators. Other variables made no significant contribution to explaining the hermit beetle occupancy. Despite the apparent univariate effect of e.g. type of wood rot, amount of wood mould, or humidity, variation within those variables might be strongly confounded with variation due to the tree species.

Several previous studies have also found tree diameter to be an important factor in determining hermit beetle occurrence (e.g. Ranius 2000; Oleksa *et al*. 2007; Chiari *et al*. 2012), but this connection is not always evident (cf. Ranius & Nilsson 1997; Ranius 2002a;
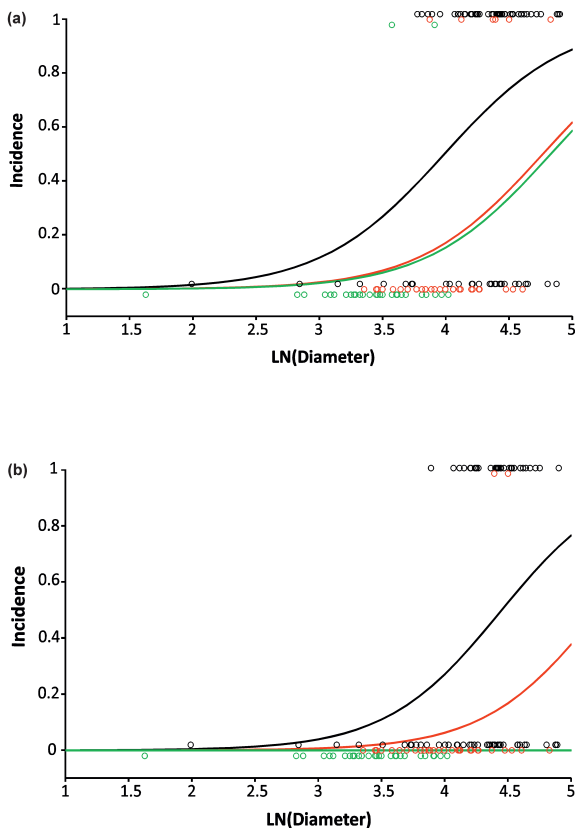
Fig. 8. The incidence of *Osmoderma barnabita* as a function of tree species and size (expressed as the natural logarithm of DBH). Shown on the y-axis are empirical observations of presences (y=1) or absences (y=0) of the species as scored by (a) larval frass versus (b) adult fragments. Included are oaks (*Quercus*; black data points); lime trees (*Tilia*; red data points) and alder (*Alnus*; green data points). Curves show fitted probabilities from a GLM (see III), with the steepest, black curves referring to incidence in oak hollows, red curves to hollows in lime, and green curves to hollows in alder. (Reproduced from Landvik *et al*. 2016. Insect Conservation and Diversity 9 (1):38–48 doi 10.1111/ icad.12141; see original article III).

Ranius *et al*. 2009b). Pedunculate oak was clearly the most abundant hollow tree species on Ruissalo Island, which may partly cause the apparent preference of *Osmoderma* for this species in the current study. Likewise, hermit beetle occurrence was mainly detected from roadside trees in northern Poland, where lime trees (*Tilia cordata*) comprised the most abundant hollow tree resources (Oleksa *et al*. 2007). Thus, tree species occupied by *O. barnabita* might not demonstrate exact specialisation on a certain host tree species, but more likely resources which are easily available in the long term.

The current results may also have been influenced by our new sampling techniques, by the structure of local biological communities, and by the recent succession of the study site. In terms of sampling, our vacuum cleaner approach allowed us to collect wood mould material from a majority of tree hollows available, including very narrow and deep hollows (Fig. 4). Previously, the occupancy of such small cavities may have been underestimated in almost all *Osmoderma* sp. habitat studies (cf. Ranius & Nilsson 1997; Vignon 2008; Oleksa 2009; Ranius *et al*. 2009b; Ranius *et al*. 2011). In terms of impacts from the surrounding communities, vertebrate nesting and hibernation was observed in several small cavities (M. Landvik, personal observations), which can have an influence on the quality and quantity of wood mould (cf. **IV**). Vertebrate animals (i.e. Aves, Mammalia) can act as facilitators, transporting plant-derived subsidies from outside the tree hollows, consequently improving local wood mould quality in smaller tree cavities (cf. **IV**). These types of effects may have influenced the presence of *Osmoderma* in several hollow types, by weakening the association between cavity size, wood mould volume, and the size of the entrance hole (cf. Ranius & Nilsson 1997; Ranius et al. 2009b). The tree hollow habitat is also an example of a long-lasting resource which may remain for decades or even centuries (Ranius *et al*. 2009b). Therefore, in some cases current presence of the hermit beetle may indicate past habitat quality (Dubois *et al*. 2009). In Ruissalo, the presence of the species (in the form of larval frass, chitin fragments, and live imagos) was observed in many previously open woodlands (M. Landvik, personal observations), which have since changed into more closed woodland (cf. Vuorela 2000, 2001). Thus, succession of the study sites may have distorted results in cases where the environment has rapidly changed but *Osmoderma* (or signs of it) still remains in the habitat as remnant populations (cf. Dubois *et al*. 2009). The extent to which current occupancy patterns reflect past habitat conditions is an issue calling for urgent attention.

The sampling methods employed here (presence of larval frass, and adult chitin fragments) lacked resolution to reveal the exact number of beetle individuals sustained by a host tree. Nonetheless, since our samples were explicitly collected from the surface of the wood mould rather than deeper down, they offer relatively reliable indicators of the recent presence of the study species. Many trees for which the presence of *Osmoderma* was thus established are located in semi-open (48 %) and open (38 %) environments,

as standing on roadsides, in parks, in private yards, or on a golf course (M. Landvik, unpublished data). Such sites are particularly problematic when it comes to conservation management, since decaying trees can be seen as a threat to people, commonly causing conflicts (cf. Carpaneto *et al*. 2010; Nieto & Alexander 2010; Stokland *et al*. 2012). At the same time, the adequacy of nature reserves may deteriorate if veteran tree supplies decrease because of poor insolation, higher mortality, and competition of surrounding vegetation (cf. Ranius & Jansson 2000; Drobyshev *et al*. 2008; Koch Widerberg 2013; Šebek 2016). Thus, the conservation of the hermit beetle should be focused on securing an abundant supply of veteran trees (i) by minimising the mortality rate of old and large-sized deciduous tree individuals, and (ii) by refraining from removing old and large-sized deciduous trees in cultural habitats (cf. Ranius 2000; Vuorela 2001; Drobyshev *et al*. 2008; Ranius *et al*. 2009a; Nieto & Alexander 2010).

4.4   Habitat use by the hermit beetle (IV)

4.4.1   Larval growth and mortality (IV)

The main substrates (brown-rot wood, larval frass, leaf humus) differed substantially in their elemental composition (see **IV** Appendix, ESM1). Elemental levels were clearly lowest in brown-rot oak wood (excluding carbon concentration), while larval frass and leaf humus proved rich in many elements. Leaf humus contained the highest values (mg/kg) of most chemical elements (As, B, Ca, Cd, Cu Fe, Mg, Mn, Na, Ni, Si, Zn), with larval frass showing higher values for some elements (P, K, S, N). However, our experimental design prevented us from inferring true causal links between larval growth and individual elements (see **IV** appendix, ESM1).

In the larval rearing experiments (**IV**) the effect of increasing the proportion of leaf humus was modified by the fraction of frass in the substrate. This held true for larval mass increase, for the probabilty of reaching higher instar and for the survival of larvae (significant two-way interactions Leaf humus × Larval Frass; Fig. 9). Brown-rot wood was the poorest substrate for gaining larval mass, for enhancing larval instars, and for promoting larval survival. Therefore, the cavity walls of a hollow do not offer many nutrients for the larvae (cf. Luce 1996; Ranius *et al*. 2005; Siitonen 2012a), and accumulating debris can be more important to hermit beetle development. In this current case, genus *Osmoderma,* as belonging to the taxa Scarabaeidae, is actually exploiting the normal dietary source of its family – i.e. faeces of other animals and plant debris (cf. Simmons & Ridsdill-Smith 2011; Schoolmeesters 2017). Thus, it is not surprising that the hermit beetle, which has generally been regarded as a wood eater (e.g. Dubois 2009; Siitonen 2012a) is actually polyphagous, having the capacity to consume a rich variety of decaying plant-derived materials.
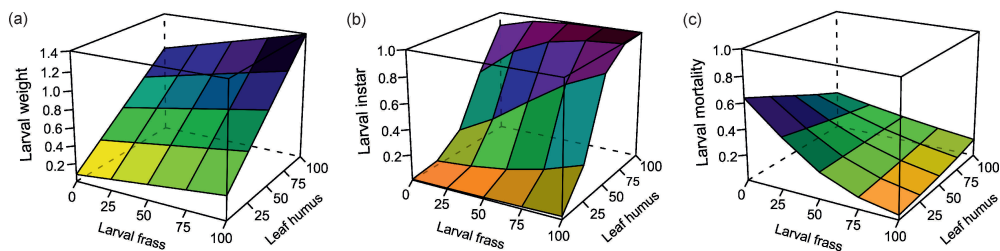
Fig. 9. Three metrics of larval performance as functions of time and growth medium in the larval rearing experiment: (a) Larval mass halfway through the experiment (week 7); (b) Larval instar at the end of the experiment (i.e. probability of transition beyond the first instar before week 13); (c) Total larval mortality by the end of the experiment (week 13). Estimates derive from least squares means of the models outlined (see IV, Table 1). Implicit in the figure is the proportion of the third component in the substrate mix, i.e. wood material affected by brown-rot wood. Thus, a substrate consisting of brown-rot wood alone is found at the point where both the proportion of leaf humus and larval frass equal zero, i.e. in the left-hand corner of the figures. (Reproduced from Landvik *et al*. 2016. Oecologia 182(1):163-175 doi 10.1007/s00442-016-3661-y; see original article IV).

Results from previous habitat studies have established that a large quantity of wood mould is a qualitative factor (cf. Hedin 2003; Chiari *et al*. 2012) which correlates with the presence of the hermit beetle in tree hollows (cf. Ranius & Nilsson 1997; Ranius 2000, 2007; Ranius *et al*. 2009b). Results of this current thesis study do not rule out the benefial effects of large wood mould quantity (physical quality), which can keep the cavity microclimate in balance, and thus act as one key factor in larval development (cf. Kelner-Pillault 1974; Vernon *et al*. 1996; Vernon & Vannier 2001; Chiari *et al*. 2012). The current results demostrate that *Osmoderma* is also able to respond to the chemical composition of wood mould, allowing the use of even small, nutrient rich cavities as habitats. Thus, the conservation of *Osmoderma* species should focus on maintaining all veteran trees, regardless of the exact size of entrance hole or the specific quantity of wood mould in the cavity (cf. **III**).

4.4.2 Microbial influence on larval growth (IV)

The relative size of the difference in larval performance between microbially infested and sterilised substrate varied in time (significant two-way interaction, Group × Week; see **IV**, Table 2). Larval growth was clearly faster (during the first two months) in unsterilised frass substrate, which led to keen preparation of wintering chambers. In sterilised frass substrate, larval growth was slow, but overall survival higher. Individuals reared in unsterilised frass would have been ready to hibernate in October-November (cf. natural conditions), whereas at this point, the larvae reared in sterilised frass were still trying to gain additional mass (see **IV**, Fig. 3a). Due to factors mentioned above, there is reason to assume that microbes may be involved in converting faecal waste to edible food, and perhaps constitute good food themselves.

All larvae fed fungal mycelium (*n*= 15) died without any noticeable growth. While the sulphur polypore (*L. suphureus*) is responsible for hollow formation in oak trees (Stokland *et al*. 2012), and mycelium-covered cavity walls are assumed to provide an important dietary source for *Osmoderma* sp. larvae (Luce 1996), my results suggest that the fungus itself is not digestible by *Osmoderma*. This finding runs contrary to previous presumptions (cf. Luce 1996), and to the mycetophagous capacities observed in some other saproxylic species (cf. Farrell *et al*. 2001; De Fine Licht & Biedermann 2012; Ulyshen 2016). Thus, observations of *Osmoderma* larvae feeding on the border of soft and hard wood (e.g. Palm 1959) will likely derive from larvae consuming bacterial conglomerates (cf. Pageix 1968) rather than fungal mycelia. Therefore, from an *Osmoderma* perspective, the prime value of fungi may likely reside in forming the hollow and a basin for the accumulation of organic debris.
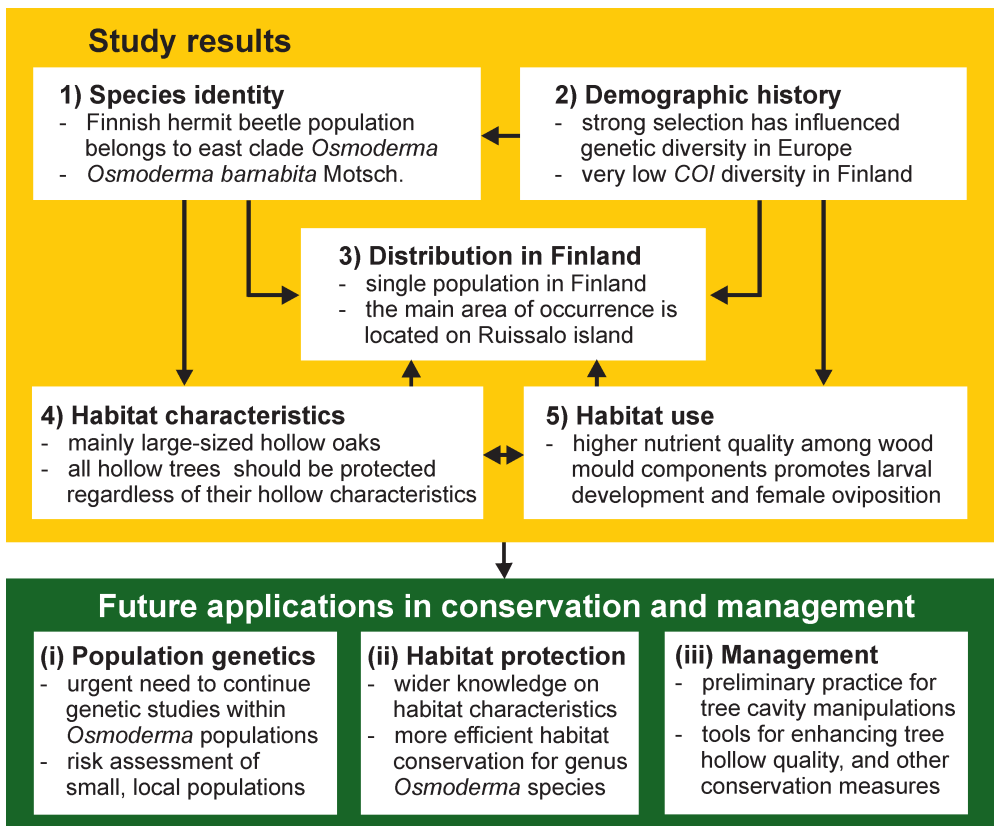
4.4.3 Female preference: oviposition test (IV)

Osmoderma females were able to assess the higher elemental quality of substrates. In the "cafeteria experiment", ovipositing females preferred leaf humus (**IV**). Females laid a total of 279 eggs (*n*= 274 hatched larvae, and *n*= 5 unhatched eggs), with the proportion of eggs differing significantly between substrates ($F_{2,72}$ = 22.51, *P* < 0.0001). All fertile females (*n*= 25) laid at least one egg in leaf humus (range 1-16), which also proved the optimal dietary source in the larval rearing experiments (cf. above). Also, the largest proportion of offspring was observed in the leaf humus substrate (*n*= 161 eggs), whereas the second most preferred substrate was larval frass (*n*= 117 eggs), and only a single hatched larva was found in brown-rot oak wood. The current results agree with the optimal oviposition hypothesis ("mother knows best"), postulating that females are able to choose resources to maximise offspring fitness (Jeanike 1978).

In terms of fertility, the mean egg load of *O. barnabita* females was quantified as 11.12 ± SD 5.45 per fertile female (range 2-21), which resembles the results with *O. eremita* (cf. Svensson *et al*. 2011). While some observations present evidence for bigger egg loads in *Osmoderma* sp., those results may be based on multiple ovulations (cf. Sweetman & Hatch 1927; Luce 1995). However, the life expectancy of females (approx. 4 weeks in natural conditions) usually confines ovipositon to a single ovulation event, with the maximal resulting egg load in *O. eremita* consisting of approximately twenty eggs (cf. Jönsson 2003; Ranius *et al*. 2005; Tauzin 2005).

5.   CONCLUSIONS AND FUTURE DIRECTIONS

In this thesis, I have identified the Finnish hermit beetle population as belonging to the cryptic species *Osmoderma barnabita* Motschulsky, 1845 within the eastern clade of *Osmoderma* (**I**). When referring to this taxon, the taxonomical synonym *Osmoderma coriarium* De Geer, 1774 should be avoided (cf. Rassi *et al*. 2015), as the collecting locality and morphology of the type specimen are not unambiguously defined (see De Geer 1774; Gusakov 2002; Audisio *et al*. 2007). The Finnish population exhibits a single mtDNA *COI* haplotype in 759 bp sequence, which appears unique in the area of the European Union. This pattern may reflect colonisation by an extremely restricted original population and/or by subsequent bottleneck effects, and by highly restricted migration among current European subpopulations (**II**). The overall *COI* diversity of *O. barnabita* decreases to the north in Europe (compared to Central and East Europe), demonstrating post-glacial expansion after the Pleistocene ice ages. The intraspecific divergences among *O. barnabita* populations indicate a rather narrow *COI* diversity, as all analysed sequences (*n*= 196, 759 bp) were separated by only one to four mutations from the central haplotype of the Baltic region. Studies related to genetic diversity should be extended, as structural changes among threatened populations should be taken into account in conservation management. In future studies, it is important to obtain samples from larger areas, and to improve genetic resolution with comprehensive gene markers. Only in this way we may establish whether the Finnish population actually suffers from deleterious effects of genetic empoverishment.

Notwithstanding the IUCN proposal that the hermit beetle may occur more widely in southern Finland (cf. Alexander *et al*. 2010), I have confirmed the Turku region as the only occurrence of the hermit beetle in Finland. Within this area, I constrained the currently known population to a square less than 10 x 10 km² (**III**). This underlines the importance of Ruissalo Island in hermit beetle conservation. Habitat studies in the main area of occupancy (Ruissalo) indicate that here, the hermit beetle occurs with a high probability in almost any large, hollow oak tree (*Quercus robur*) (**III**). In addition, evidence gained in this study showed occurrences on several other host tree species (*Tilia* sp., *Alnus glutinosa*, *Sorbus aucuparia*, *Acer platanoides*, *Populus nigra*). Thus, conservation efforts should be based on preserving all large-sized hollow trees, regardless of proven species presence, tree characteristics, or the exact environment surrounding the tree. The aim of conservation should be to secure a good supply of veteran trees, among which hollow formation is a normal process due to the presence of biotic factors. Possible differences in habitat use between cryptic *Osmoderma* species will require further comparative studies, but current similarities suggest that similar conservation measures may favour all species.

Study results

1) Species identity
- Finnish hermit beetle population belongs to east clade *Osmoderma*
- *Osmoderma barnabita* Motsch.

2) Demographic history
- strong selection has influenced genetic diversity in Europe
- very low *COI* diversity in Finland

3) Distribution in Finland
- single population in Finland
- the main area of occurrence is located on Ruissalo island

4) Habitat characteristics
- mainly large-sized hollow oaks
- all hollow trees should be protected regardless of their hollow characteristics

5) Habitat use
- higher nutrient quality among wood mould components promotes larval development and female oviposition

Future applications in conservation and management

(i) Population genetics
- urgent need to continue genetic studies within *Osmoderma* populations
- risk assessment of small, local populations

(ii) Habitat protection
- wider knowledge on habitat characteristics
- more efficient habitat conservation for genus *Osmoderma* species

(iii) Management
- preliminary practice for tree cavity manipulations
- tools for enhancing tree hollow quality, and other conservation measures

Fig. 10. Schematic image presenting the main conclusions of the thesis, with future approaches. Arabic numbers (1–5) refer to study aims on page 18-19, with future approaches and needs shown by numbers i–iii at the bottom.

My current results support the ability of adult females to respond to the chemical quality of wood mould components (**IV**). A rich elemental composition and naturally existing bacteria in wood mould can promote *O. barnabita* larval development, and similarly female choice of oviposition seems to reflect such demands. Thus, the current study provides a preliminary answer to the question of how a cavity becomes a "good hollow" for *Osmoderma*. The evidence gained can be used in enhancing cavity microhabitats in the species' current area of occurrence, in translocations, in surrogate boxes and when constructing ecological corridors. Even so, more studies are needed to reveal the long-term influences of "cavity manipulation" on *Osmoderma* and other saproxylic species.

Overall, the conservation of saproxylic species in urban environments is challenging, since the target species are associated with dead or decaying wood (Nieto & Alexander 2010), and as some of the hollow trees exploited by the hermit beetle may be of a very high age (200–500 years; Ranius *et al*. 2009a; Ranius *et al*. 2009b). In urban risk assessment, even trees younger than 100 years are often removed for posing a threat to people (cf. Jokinen 2017; Mäkinen 2017). Nonetheless, the maintenance of old

trees should be a priority in urban species conservation, and tree removals should be accepted only as the last resort (cf. Stokland *et al*. 2012; Roloff 2016). In Ruissalo, the threat to the hermit beetle has presumably increased as the main population (86 %) is occupying large trees on roadsides, in parks and private yards, and on a golf course (M. Landvik, unpublished data). Decaying veteran trees and people rarely agree very well, which frequently results in conflicts. In contrast, a small proportion (14 %) of the tree-level occurrences of *Osmoderma* still exists in strictly protected nature reserve forests, the closed structure of which may not be the optimal environment for the hermit beetle (M. Landvik, unpublished data). While my current results suggest that the species is highly insensitive to local environmental conditions, part of this patterns may be due to remnant populations lingering on in successional habitats turned less suitable (cf. Dubois *et al*. 2009). Under this view, active conservation management should be introduced to decrease the mortality rate of veteran trees and to facilitate tree regeneration by improving openness in closed forests (Ranius *et al*. 2005; Drobyshev *et al*. 2008; Ranius *et al*. 2009a; Stokland *et al*. 2012). This strategy can promote stability in veteran tree supplies, but can also increase saproxylic species diversity in temperate semi-urban forests (e.g. Vodka *et al*. 2009; Koch Widerberg *et al*. 2012; Horák & Rébl 2013; Horák *et al*. 2014; Lachat *et al*. 2016). Active forest management should be based on systematical and permanent actions in man-made landscapes, e.g. in small oak stands and wood pastures in order to avoid biodiversity loss (cf. Vuorela 2001; Lassauce *et al*. 2011; Koch Widerberg 2013; Šebek 2016). Therefore, to sustain a rich biodiversity in a former cultural landscape, collaboration among scientists, local authorities and residents is required along with mutual agreement on targets and goals.

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