Forest dieback in a protected area triggers the return of the primeval forest specialist *Peltis grossa* (Coleoptera, Trogossitidae)

**Abstract**

Forest set-aside is a commonly employed conservation strategy, but large-scale disturbances regularly evoke discussions on its utility for biodiversity conservation in former production forests. In this study, we reconstructed the return of a primeval forest specialist, the beetle *Peltis grossa* (Linnaeus, 1758) of the family Trogossitidae, to two national parks after more than a century of absence. To illuminate historical processes and the role of potential refuges and species' size, we compared the beetle's current distribution collected in a large-scale citizen science approach, with historical data and the current distribution of two closely related, smaller species. We quantified deadwood preferences and investigated the effect of benign neglect versus salvage-logging management practices on *P. grossa* abundances. Our findings support the view that *P. grossa*...
survived in the southern Bohemian Forest, which enabled its recolonization of the landscapes. However, a build-up of the population was dependent upon a massive supply of deadwood by bark beetles within the refuge area. In a large area in the north of the study region that >20 years ago contained ample amounts of deadwood, forest succession outpaced colonization by *P. grossa*. The current probability of the species’ presence decreased with distance to the presumed refuge area from 70% to 5% at 40 km. In the present core distribution area of *P. grossa*, salvage logging reduced its abundance by the factor 20. These results provide three important lessons on the potential of natural disturbances as a biodiversity restoration tool in forest set-asides: First, large supply of deadwood by disturbance can trigger the return of locally extinct primeval forest specialists. Second, the species must survive within a critical distance (for *P. grossa* < 10–40 km). Third, salvage logging significantly reduces the population densities of forest specialists by reducing habitat amount.

**KEYWORDS**
benign neglect strategy, citizen science, salvage logging, urwald relict species

### 1 | INTRODUCTION

#### 1.1 | Biodiversity conservation in formerly commercial forests

The designation of strictly protected areas is a common approach in attempts to maintain and promote biodiversity. In Europe, and especially in Germany, a large proportion of these protected areas are forests (BMEL, 2017; Europäische Kommission, 2016). Among the total forested area in the temperate zone of Europe, undisturbed natural forests make up only 0.4% (Parviainen, 2005). Consequently, protected forest areas are predominantly commercial forests, which differ from natural forests in their tree species composition, mainly conifers rather than broad-leaved trees (Schelhaas et al., 2003). Additionally, commercial forests are impoverished in their deadwood amount and diversity, the result of centuries of regular timber harvest and sanitary cuttings to prevent pest outbreaks and remove threats to public safety (Merganičová et al., 2012; Thorn et al., 2020). Globally, this has finally led to a lack of old and over-mature trees offering diverse deadwood microhabitats (Larrieu et al., 2014; Lindenmayer et al., 2012; Miklín et al., 2018; Speight, 1989). These forest alterations predominantly affect wood-inhabiting specialist species (Grove, 2002; Seibold et al., 2015). Whether the designation of strictly protected areas in formerly managed forests is conducive to biodiversity conservation and whether the protection of natural processes provides natural habitat amounts to re-establish extinct deadwood specialists are thus far unclear.

#### 1.2 | Natural disturbances and benign neglect strategy

In European forests, management practices and climate change are drivers of an altered disturbance regime that have led to increased damage (Seidl et al., 2011). Windthrows, common in monocultures, even-aged, dense stands, and higher-age stands (Schelhaas et al., 2003), together with drier summers have increased the occurrence of bark beetle outbreaks (Pfeffer & Skuhryvá, 1995). To avoid bark beetle infestations of adjacent forests and to capture economic return from disturbance-affected stands, salvage logging (Dobor et al., 2019) has been widely implemented not only in Europe but also in Asia, even in protected areas (Müller et al., 2019). However, postdisturbance logging compromises the aim of the protected areas by adversely affecting many ecosystem functions (Leverkus et al., 2018) as well as the biodiversity of saproxylic, that is, deadwood dependent, species (Thorn et al., 2018).

Modern forestry has caused the loss of deadwood specialist species, such as the beetle species *Pytho kolwensis* (Sahlberg, 1833) and *Rhysodes sulcatus* (Fabricius, 1787), which went extinct in parts of Scandinavia (Siitonen & Saaristo, 2000; Speight, 1989). However, there is limited
empirical evidence of the conservation benefits provided by a management strategy based on the benign neglect of former commercial forests (Della Rocca et al., 2014; Doerfler et al., 2020; Hagge et al., 2019)—in which natural processes are left to natural succession—and the efficacy of this strategy is accordingly still under debate (Hlášy et al., 2021; Müller et al., 2010). In one of the few examples of successful bark beetle neglect management, the wood-inhabiting fungus *Antrodiaella citronella* (Niemelä & Ryvarden, 1983) was able to re-establish its population in south-eastern Germany, based on small relict populations (Bässler & Müller, 2010). Nonetheless, a broader evaluation of the full potential of disturbances in bark beetle neglect approaches requires a determination of the conditions and time span necessary for biodiversity maintenance in formerly commercial forests.

### 1.3 Peltis grossa: A primeval forest relict beetle

The Bohemian Forest is the largest continuous forest area in Central Europe (Bässler et al., 2008). It includes two adjoining national parks, the Bavarian Forest National Park (Germany) and Šumava National Park (Czech Republic), founded in 1970 and 1991, respectively. Both were previously known to harbor numerous saproxylic beetle species of high European conservation concern, such as *Lacon lepidopterus* (Panzer, 1801), *Boros schneideri* (Panzer, 1795), and *P. grossa* (Fleischer, 1927; Procházka et al., 2020; Thiem, 1906). The Bohemian Forest has recently suffered the largest natural disturbances in Europe, with two major bark beetle (mainly *Ips typographus* (Linnaeus, 1758)) outbreaks occurring in the last two decades (Schelhaas et al., 2003; Seibold et al., 2015; Thorn et al., 2017). These and other natural disturbances together with a neglect management strategy in the core zones of the national parks have led to an increase in the amount of deadwood, from which some deadwood specialists such as *Cerhus chrysomelinus* (Hochenwarth, 1785), *Ambedus auripes* (Reitter, 1895), and *Danosoma fasciata* (Linnaeus, 1758) have profited whereas other species, including *Lacon lepidopterus* and *Boros schneideri*, have not (Müller et al., 2010). In 2018, *P. grossa*, a primeval forest relict beetle species, was rediscovered in Šumava National Park after nearly a century of absence (Procházková et al., 2020). One year later, the beetle was also rediscovered in the Bavarian Forest National Park, after 113 years of absence (Müller, 2020; Thiem, 1906). Despite an enormous supply of deadwood resulting from natural disturbances in form of windthrow and consecutive bark beetle outbreaks in the 1990s, *P. grossa* could not be found, despite intensive searching. The reason for its re-emergence 20 years later raises questions regarding the cause of the beetle’s delayed return and the ongoing absence of other deadwood-dependent species.

To better understand the processes underlying this successful natural recolonization of strictly protected areas, we reconstructed the temporal changes in the *P. grossa* population in the Bavarian Forest and Šumava national parks in the context of changing forest management practices. Historical distribution data were compared with the recent findings obtained in a region-wide citizen science monitoring effort and with standardized data from forests within the current core distribution of *P. grossa* in our study region, including naturally disturbed forests and forests with subsequent salvage logging. Based on the knowledge that larger saproxylic species are more prone to extinction than smaller ones (Hagge et al., 2021; Seibold et al., 2015), the study of habitat preferences and the citizen science monitoring effort included two smaller species from the Trogossitidae family, *P. ferruginea* (Linnaeus, 1758), and *Thymalus limbatus* (Fabricius, 1787), to compare the effects of changing forest management on deadwood specialists of different body sizes. The specific aims of our study were to answer the following questions: (i) where was the refuge of *P. grossa* during its presumed extinction from the Bavarian Forest and Šumava national parks? (ii) What distance, trunk diameter, and time span restrict recolonization? (iii) How do current salvage logging practices affect the local density of *P. grossa*?

### 2 METHODS

#### 2.1 Species

*Peltis grossa* (L., 1758), a beetle species of the Trogossitidae family, has been recorded in 21 European countries (Procházková et al., 2017). In Germany, its current distribution is limited to the Bavarian Forest National Park and the Alps (Müller et al., 2005). In the Czech Republic, recent findings after 2000 are scattered across the country and include Boubín (Čertova stěna) and Žofinský prales in the vicinity of the Šumava National Park (Kment et al., 2017). Due to its relatively large size (11–19 mm), it is easily distinguished from two closely related species *P. ferruginea* (L., 1758) (7–10 mm) and *T. limbatus* (F., 1787) (5–7 mm). All three species breed in brown-rotten deadwood and feed on polypore fungi like *Fomitopsis pinicola* (Swartz: Fr.) P. Karsten (Horion, 1960; Kolibáč, 2006; Procházková et al., 2017; Šmahel et al., 2020; Thiem, 1906). The Bohemian Forest is the largest continuous forest area in Central Europe (Bässler et al., 2008). It includes two adjoining national parks, the Bavarian Forest National Park (Germany) and Šumava National Park (Czech Republic), founded in 1970 and 1991, respectively. Both were previously known to harbor numerous saproxylic beetle species of high European conservation concern, such as *Lacon lepidopterus* (Panzer, 1801), *Boros schneideri* (Panzer, 1795), and *P. grossa* (Fleischer, 1927; Procházka et al., 2020; Thiem, 1906).

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To better understand the processes underlying this successful natural recolonization of strictly protected areas, we reconstructed the temporal changes in the *P. grossa* population in the Bavarian Forest and Šumava national parks in the context of changing forest management practices. Historical distribution data were compared with the recent findings obtained in a region-wide citizen science monitoring effort and with standardized data from forests within the current core distribution of *P. grossa* in our study region, including naturally disturbed forests and forests with subsequent salvage logging. Based on the knowledge that larger saproxylic species are more prone to extinction than smaller ones (Hagge et al., 2021; Seibold et al., 2015), the study of habitat preferences and the citizen science monitoring effort included two smaller species from the Trogossitidae family, *P. ferruginea* (Linnaeus, 1758), and *Thymalus limbatus* (Fabricius, 1787), to compare the effects of changing forest management on deadwood specialists of different body sizes. The specific aims of our study were to answer the following questions: (i) where was the refuge of *P. grossa* during its presumed extinction from the Bavarian Forest and Šumava national parks? (ii) What distance, trunk diameter, and time span restrict recolonization? (iii) How do current salvage logging practices affect the local density of *P. grossa*?
Adult beetles can be found during the warm nights, or occasionally during daytime, between June and September, on sporocarps or on and under tree bark (Procházka et al., 2020). Their presence in an area is also evidenced by their characteristic exit holes, with a flat and a curved side (Ehnström & Axelsson, 2002). *P. grossa* is considered a primeval forest relict species whose presence indicates old-growth forests with a high degree of naturalness (Eckelt et al., 2017). It is also classified as critically endangered in the Czech and in the German Red List (Konvička, 2017; Seibold et al., 2015).

### 2.2 Study area

The Bohemian Forest is the largest continuous forest area in Central Europe (Bässler et al., 2008). Sampling plots were chosen based on the availability of suitable forest habitats and spread over the Bavarian Forest (24,250 ha) and Šumava National Parks (68,064 ha) but were also located in several surrounding areas. Both national parks are dominated by the tree species *Picea abies* (Linnaeus) H. Karsten and *Fagus sylvatica* (Linnaeus, 1753) and have been subject to two severe windthrow events followed by bark beetle infestations in 1996–2000 and 2005–2009 (Jonáš & Prach, 2008; Seidl et al., 2015; Zemek & Herman, 2001). Both parks comprise unmanaged core areas, as well as more intensely managed zones where salvage logging is a common practice.

### 2.3 Historical and recent distribution

The historical distribution of *P. grossa* was identified from the literature (Hennvogl, 1905; Horion, 1960; Kment et al., 2017; Thiem, 1906). Recent distributions of *P. grossa*, *P. ferruginea*, and *T. limbatus* were monitored using a citizen science approach (Figure 1). Volunteers and entomologists (CZ: 15, GER: 21) were trained to recognize the adults and exit holes of the three species and followed a standardized monitoring protocol. Between June and September 2020, monitoring plots (CZ: 50, GER: 54) were visited for 45 min between 9 and 12 p.m. during nights with sunset air temperatures >19°C. Random findings were also included in the distribution map to represent the recent distribution of the three species in the Bohemian Forest (~ 100,000 ha). The distance of each *P. grossa* finding from the suspected refuge area in the border triangle was calculated using the distCosine-function in R (package “geosphere” [Hijmans, 2019]). A generalized linear model (GLM, family = “binomial”) was used to model *P. grossa* occurrence in dependence of distance to the refuge area. A distance-decay plot was used to visualize the occurrence probability of *P. grossa* with increasing distance to the refuge area. To test for an effect of trunk diameter on the occurrence of *P. grossa*, *P. ferruginea*, and *T. limbatus*, 164 tree diameters at breast height (DBH) of potential deadwood habitats were measured exemplarily at four sites of their co-occurrence in Šumava National Park during August 2020. In these four sites, all dead and partly dead trees and their parts were visually inspected on warm nights for the presence of *P. grossa*, *P. ferruginea*, and *T. limbatus*. Significant differences between beetle occurrence and trunk diameter were tested with a t test for each of the three species respectively.

### 2.4 Forest management

The influence of forest management practices, that is, benign neglect versus salvage logging, on local population sizes in *P. grossa* was investigated along the border (Austria, Czech Republic, Germany). In this region, salvage logging reduces the amounts of deadwood on average from 300 to 50 m³ ha⁻¹ (Thorn et al., 2015) and the two management practices are typically in close proximity due to differences in ownership and utilization. At six sites within a 4.2-km
range, adjacent unmanaged and managed forests were monitored for *P. grossa* in a 20-min search per site on August 8, 2020, between 9 and 11 p.m. Paired forest plots were ~200 m apart and monitored simultaneously by teams of two expert taxonomists. To test for an effect of forest management on *P. grossa* abundance, a paired *t* test was applied.

### 3 | RESULTS

#### 3.1 | Historical distribution

In the Bohemian Forest area, historical records of *P. grossa* exist for the period 1905–1919 (Figure 2) (Hennvogl, 1905; Horion, 1960; Kment et al., 2017; Thiem, 1906). Within the areas currently protected as national parks, the beetle vanished nearly simultaneously, with the last records dating back to 1906 (GER) and 1912 (CZ) (Figure 2a). By contrast, *P. ferruginea* and *T. limbatus* were never considered extinct in the area, but historical records indicate that *P. ferruginea* was previously common throughout Germany while *T. limbatus* occurred only sporadically (Horion, 1960).

#### 3.2 | Recent distribution, habitat requirements, and forest management

The recent distribution of *P. grossa* is centered on the southern part of Šumava National Park, based on an accumulation of findings in the border triangle (Figure 2a). Monitoring revealed *P. grossa* in four of the 54 monitoring areas (7%) in the Bavarian Forest National Park, and in 8 of the 50 monitoring areas (16%) in Šumava National Park. Additionally, in Šumava National Park many random findings occurred during daytime, providing evidence for the presence of *P. grossa* in 115 of 318 (36%) visited sites. Additionally, eight verifications were acquired outside the parks (A: 1, CZ: 4, GER: 3) (Figure 2a). *P. ferruginea* and *T. limbatus* were more
common than *P. grossa* in the study area, especially in the north of Šumava National Park and across the entire Bavarian Forest National Park (Figure 2b,c). Of the latter two beetle species, *P. ferruginea* occurred in more of the sampling sites than *T. limbatus* (Figure 2b,c).

To identify the dispersal limits of *P. grossa*, we calculated the distance–decay curve emanating from the current core distribution area in the border triangle (Figure 3). The most distant record from the core distribution was 66 km toward the north in the Šumava National Park. The probability of the species’ presence decreased as a function of the distance from the core distribution site, from 70% to 5% at 40 km (Figure 3). An investigation of trunk diameter revealed that *P. grossa* and *P. ferruginea* exhibit a preference for deadwood with larger trunk diameter (Figure 4a). A comparison of two forest management practices with local population sizes of *P. grossa* showed a 20-fold reduction in abundance of salvage logging sites compared to benign neglect (Figure 4b). In fact, in half of the considered salvage logging sites, *P. grossa* could not be detected at all.

Moreover, local densities were much lower in areas of salvage logging than in areas with benign neglect management.

### 4 | Discussion

*P. grossa* survived probably unnoticed in the Bohemian Forest, namely in the southern part of Šumava National Park. The beetle’s presumed recolonization of the northern part of the Bohemian Forest is recent, occurring after over a century of the species’ absence. However, the distribution of *P. grossa* is effectively limited to a distance of <40 km.

4.1 | Citizen science

*P. grossa* monitoring turned out to be highly attractive for the participants. This no doubt reflected the recent sensitization of the public to the issue of insect decline (Hallmann et al., 2017) and particularly an increasing awareness of saproxylic beetles in both national parks, for example, through children’s books, stamps, newspaper articles, and podcasts (Thorn et al., 2020). Similar successful efforts to train citizens in saproxylic beetle monitoring, including species of high European conservation concern, have been reported by Méndez et al. (2017) and Zapponi et al. (2017). Our approach adds two additional lessons to the applicability of citizen science to saproxylic beetles: First, citizen science is even possible under difficult conditions, e.g. during the night in remote areas with more than 300 m³ deadwood/ha. Second, volunteers of all ages can be inspired to search for the rarest species, which demonstrates a great potential for education and public relations improving the acceptance of natural processes in strictly protected areas (Müller et al., 2019). In the long-run, training citizens to identify species of conservation concern will boost the distribution data and will allow to track the ongoing recovery of species as *P. grossa* in time and space.
4.2 Source population

Data compiled from the literature support the view that *P. grossa* was widely distributed in the Bohemian Forest in the beginning of the 20th century (Hennvogl, 1905; Horion, 1960; Kment et al., 2017; Thiem, 1906), when natural forests were still abundant (Hennvogl, 1905). The current distribution of *P. grossa* collected in the Bohemian Forest area suggests a source population in the border triangle where densities are currently at their highest. Whether the source population has always been there unnoticed due to its low densities, or re-emerged only recently from stable populations outside the national parks, is thus far unclear. The two closest potential recent reservoirs are Čertova Stráň, located near the Boubín Virgin Forest, and the Žofín Forest Nature Reserve (Boháč & Matějíček, 2004; Kment et al., 2017). Čertova Stráň, at a distance of 25 km from the border triangle, is within the confirmed dispersal range of 40 km (Figure 3) whereas Žofín Forest Nature Reserve is about 65 km away. A subrecent population of *P. grossa* close to the Bohemian Forest (about 60 km away) is known from the game enclosure near Hluboká nad Vltavou, with the last record from the year 1972 (Z. Kletečka, pers. comm.). The populations around the river Střela about 140 km northwest from the border triangle (Týr, 2011) and in the Alps (Müller et al., 2005), >160 km away, are unlikely source populations because the great distance is presumably prohibitive for a habitat specialist such as *P. grossa*, given the absence of step-stone habitats (Rink & Sinsch, 2007). In conclusion, the pattern suggests that a refuge in the old-growth forest at Mt. Plechý in the border triangle (Bässler et al., 2011) is most probable.

4.3 Habitat renewal and continuity

Based on the life cycle and feeding habits of *P. grossa*, its occurrence can be linked to large-diameter deadwood inhabited by polypore fungi such as *Fomitopsis pinicola*, *Fomes fomentarius* (Linnaeus: Fr.) Kickx, and *Piptoporus betulinus* (Nikitsky & Schigel, 2004; Schigel, 2002), which we could confirm in our monitoring. In the Bohemian Forest, the return of *P. grossa* was likely made possible by two disturbance events in the 1990s and 2000s that provided deadwood in amounts unprecedented since the founding of the two national parks (Thorn et al., 2017), where core zones with benign neglect management have allowed natural succession. The common occurrence of the fungus-distributing beetle *Hylurgops palliatus* (Gyllenhal, 1813) facilitated the early colonization of *F. pinicola* at high abundances within 1 year after a bark beetle outbreak (Vogel et al., 2017; Weslien et al., 2011). However, *P. grossa* takes 2–3 years in its development (Ehnström & Axelsson, 2002) and recolonization by it only begins 10 years after tree death (Weslien et al., 2011). Comparable long establishment times are known from the saproxylic beetle *Cerambyx cerdo* (Linnaeus, 1758) (Drag & Cizek, 2015), demonstrating that a long-term habitat continuity is a major limiting factor for many of the less mobile saproxylic insect species found throughout most of western Europe (Grove, 2002). A disruption of continuity was shown to have immediate negative effects on *Pytho kolwensis* (Siitonen & Saaristo, 2000) and other saproxylic habitat-specialists (Laaksonen et al., 2020).

4.4 Arrival of *P. grossa* at new habitats

For the successful return of *P. grossa* to the Bavarian Forest National Park in the 49th year after the park’s establishment, the beetle had to reach the newly formed habitats at the proper stage of forest succession, that is, 10 years after tree death. The first detections of *P. grossa* in 2018/2019 followed the disturbance event caused by the windstorm Kyrril in 2007 (Procházka et al., 2020). This raises the question why *P. grossa* did not exploit the deadwood wave that occurred in the 1990s. The beetle was intensely searched for in the Bavarian National Park (Müller et al., 2010) and had not been noticed previously in bark beetle pheromone traps that were set up in Sumava National Park. That *P. grossa* remained locally extinct during the deadwood wave in the 1990s can be explained by density-dependent dispersal limitation (Travis et al., 1999). In other words, at the beginning of the 21st century, the density of the source population was below a threshold density, beneath which no effective emigration from the refuge occurs (Poethke & Hovestadt, 2002). This reflects the fact that one of the most critical parameters determining successful dispersal is the size of a local population and its dependence on high quality habitat with sufficient amount (Komonen & Müller, 2018; Seibold et al., 2017). This has been demonstrated for the rare saproxylic beetle *Pytho kolwensis* requiring an amount of more than 70 m$^3$ ha$^{-1}$ in Finish spruce forests (Siitonen & Saaristo, 2000). The disturbances in the 1990s did not allow an accumulation of the required quantities of deadwood in the presumed refuge until the mid-2000s, which then seems to have triggered the presumed recolonization of the larger landscape. In the recent distribution range of *P. grossa*, the beetle’s occurrence probability declined rapidly within a 40-km radius from the assumed source population in the border triangle. A recent review of the dispersal distances of saproxylic insects identified...
restrictions for beetle species at roughly ≥ 10 km (Komonen & Müller, 2018), a finding well supported by our study. Compared to other taxa, such as fungi, beetles are generally considered to have a lower dispersal power (Komonen & Müller, 2018). This is fully consistent with the finding that the rare fungus *Antrodiella citronella*, also related to *F. pinicola*, was able to recolonize the entire Bohemian Forest already during the first deadwood wave in the 1990s, despite its similar restriction to two small refugia in the study area (Bässler & Müller, 2010).

In contrast to *P. grossa*, the two related beetles, *P. ferruginea* and *T. limbatus*, are regularly found throughout the Bohemian Forest. Despite their assessment as rare species of the Bohemian Forest in the middle of the 20th century (Horion, 1960), they are quite common, or even locally highly abundant, nowadays. Since, to the best of our knowledge, neither of the latter species became locally extinct, their populations were able to more quickly recover landscape in high densities when provided with a deadwood supply by the first disturbance event. Also, smaller body size is related to advantageous life traits such as shorter generation times (McKinney, 1997) and smaller species profit from shorter larval development times and can thus make use of smaller deadwood trunks, which comprise less substrate than larger ones (Brin et al., 2011). Indeed, it has been shown that higher extinction risks in saproxylic beetles are better explained by body size than by any other ecological or morphological traits (Hagge et al., 2021; Seibold et al., 2015). However, *P. grossa* is larger and depends on large-diameter trunks, which can only be reliably found in old-growth forests (Procházkova et al., 2020) or unlogged disturbance areas (Donato et al., 2012). Consequently, this beetle is more dependent on a long tradition of benign neglect management.

### 4.5 Natural disturbances and forest management

Most areas in the Bohemian Forest are used for economic purposes and in the national parks many areas are managed for reasons of bark beetle control and public safety. The negative effect of salvage logging, which on average reduces the amounts of deadwood by at least 75% (Priewasser et al., 2013; Thorn et al., 2015), on the number of *P. grossa* individuals is likely to be even larger than reported as 20-fold in our investigation, considering that the salvage logging sites in our comparison were in the direct vicinity of the unmanaged sites, from which single individuals could distribute. Bark beetle outbreaks have been shown to pose no threat to the major goals of protected areas (Kortmann et al., 2021) and new methods of bark beetle control, for example, bark scratching, do not impede the development of other saproxylic beetles (Thorn et al., 2017). With the growing number of reported disturbance events (Seidl et al., 2014), increasing evidence of the negative effects of salvage logging on threatened species and on the integrity of natural processes (Leverkus et al., 2018; Thorn et al., 2017; Thorn et al., 2018), as well as recent court rulings in which salvage logging in Natura 2000 was deemed to be unlawful (Schiermeier, 2018), post-disturbance logging is no longer an option in protected areas established to conserve a high level of biodiversity (Müller et al., 2019). Our study provides yet another demonstration that salvage logging is detrimental to highly threatened species, by reducing their population densities and thereby limiting recolonization. To guarantee public safety, it is sufficient to limit deadwood management to the close proximity of hiking trails (Vítková et al., 2018). Moreover, even in those areas the trees providing habitat for *P. grossa* can be left, as shown in a study using artificial stumps in Sweden (Weslien et al., 2011).

### 4.6 Outlook

The return of *P. grossa* is a success story for the Bavarian Forest and Šumava national parks and in the coming years the beetle can be expected to distribute gradually within the Bohemian Forest. Its return well demonstrates the potential and limitations of strictly protected areas in former commercial forests to support highly threatened forest specialists. Three important lessons for managers of strictly protected forests in Europe are provided by our study: First, *P. grossa*, while locally extinct, survived in the wider region. Second, there was a drastic increase in habitat amount in the presumed refugial area, which allowed the species to reach a high local abundance after 10 years of wood decay. Third, in the landscape, including that in the Bavarian Forest and Šumava national parks, deadwood was repeatedly enriched over decades by natural disturbance events, such as windthrows and bark beetle eruptions, which provided suitable substrate when *P. grossa* newly reached the area. For other remnant populations of saproxylic beetles, forest management at their refugia should include the repeated enhancement of local habitat amounts based on measures that recognize the long (~10 years) period of time required for the development of suitable deadwood habitats. Increasing disturbances under benign neglect management offer the simplest method to achieve this goal.
ACKNOWLEDGMENTS
The authors thank our volunteers Pavel Bečka, Samantha Biebl, Michala Bryndová, Ladislav Černý, Miroslav Černý, Jaroslav Červenka, Vít Chlada, Kristýna Falková, Jiří Flousek, Michael Großmann, Lukas Haselberger, Julia Herzig, Werner Kirchner, Achim Klein, Jochen Linner, Thomas Michler, Jan Mokrý, Cítrad Moulis, Marco Müller, Annette Nigl, Tomáš Peterka, Björn Poelzing, Jens Schlüter, Pavla Staňková, Martin Stary, Jiří Tůma, Jiří Vávra, Oldřich Vojtěch, Stěpánka Vojtěchová, Jiří Zelenka, and Jitka Ženáhlíková, without whom this extensive monitoring would not have been possible. This paper was partly supported through the institutional support of long-term conceptual development of research institutions provided by the Ministry of Culture (ref. MK000094862) and by Institutional subsidy VUKOZ-IP-00027073.

CONFLICT OF INTEREST
The authors have no conflict of interest to declare.

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How to cite this article: Busse, A., Cizek, L., Čížková, P., Drag, L., Dvorak, V., Foit, J., Heurich, M., Hubený, P., Kašák, J., Kittler, F., Kozel, P., Lettenmaier, L., Nigl, L., Prochážka, J., Rothacher, J., Straubinger, C., Thorn, S., & Müller, J. (2022). Forest dieback in a protected area triggers the return of the primeval forest specialist *Peltis grossa* (Coleoptera, Trogossitidae). *Conservation Science and Practice*, 4(2), e612. [https://doi.org/10.1111/csp2.612](https://doi.org/10.1111/csp2.612)