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Conservation value of forests attacked by bark beetles: Highest number of indicator species is found in early successional stages

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ABSTRACT

Heavy natural disturbance in large protected areas of former commercial forests increasingly evokes European parliaments to call for management intervention because a loss of habitats and species is feared. In contrast, natural early successional habitats have recently been recognised as important for conservation. Current knowledge in this field mostly results from studies dealing only with selected taxa. Here we analyse the success of species across 24 lineages of three kingdoms in the Bavarian Forest National Park (Germany) after 15 years of a European spruce bark beetle (*Ips typographus* L.) outbreak that led to rapid canopy opening. Using indicator species analysis, we found 257 species with a significant preference for open forests and 149 species with a preference for closed forests, but only 82 species with a preference for the stand conditions transitional between open and closed forests. The large number of species with a preference for open forests across lineages supports the role of this bark beetle as a keystone species for a broad array of species. The slowdown of the outbreak after 15 years in the core zone of the national park resulted in less than half of the area being affected, due to variability in stand ages and tree species mixtures. Our case study is representative of the tree species composition and size of many large protected montane areas in Central European countries and illustrates that (1) natural disturbances increase biodiversity in formerly managed forests and (2) a montane protected area spanning 10,000 ha of low range mountains is likely sufficient to allow natural disturbances without a biased loss of closed-forest species.

Introduction

Natural forests are characteristically dynamic and heterogeneous as a result of natural disturbance regimes operating on a wide range of spatial scales. These dynamics, in contrast to intensively managed forests, lead to numerous "biological legacies" that enhance biodiversity (Franklin et al., 2000; Hunter, 1990; Noss & Cooperrider, 1994). Among ecologists, the importance of natural dynamics for enhancing biodiversity is not questioned (Hyvärinen et al., 2006; Noss & Lindenmayer, 2006) but for many people, even those active in conservation, such "damaged" forests are considered to have lost old-growth value or are no longer attractive (Burton, 2006; Chan-McLeod, 2006; Swanson et al., 2011). For this reason and especially for managers of conservation areas, ecological research must crucially provide evidence of the restorative and biodiversity-enhancing effect of natural disturbances (Lindenmayer et al., 2006). This is becoming more important because increasing disturbances have evoked broad discussions on the necessity of salvage logging as well as preventative logging across protected areas in Europe. This debate is becoming more heated because of economic constraints and the interests of lumber companies, who use terms such as "destroyed habitats" and "loss of biodiversity" (Lindenmayer et al., 2004; Stokstad, 2006).

In both Europe and North America, large disturbance events have become more frequent in recent decades (Raffa et al., 2008; Seidl et al., 2011). One cause is the increase in the proportion of mature, often planted conifer stands, which are particularly susceptible to bark beetles. The majority of the large protected areas in Europe in remote mountain areas today have high proportions of Norway Spruce (*Picea abies* (L.) Karst.) or Scots Pine (*Pinus sylvestris* L.) in particular, making up a quasi-boreal forest. Such coniferous stands are highly susceptible to natural disturbances by bark beetle infestation and windthrow (Seidl et al., 2011; Svoboda et al., 2012). Another cause of the increase in large disturbance areas is the suppression of smaller natural disturbances by beetles or fires in past decades (Raffa et al., 2008). In addition, climate-warming supports

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beetle population growth, fires, and increased windthrows (Seidl et al., 2011). If these disturbed areas are left alone to develop naturally, the area of early successional forest ecosystems increases. The ecological importance of early successional forest ecosystems as a result of natural dynamics has received little attention in conservation, and the role of these ecosystems in the maintenance of biodiversity is still underestimated (Swanson et al., 2011).

The bark beetle *Ips typographus* (L.) is one of the main drivers of disturbance in spruce-dominated forests in Europe (Müller et al., 2008). The extent and speed of bark beetle population growth depends on forest stand characteristics, such as tree species composition and age of the stands (and the total stock available). This normally leads to a strong spatial heterogeneity of recovery processes, and therefore the early successional phase is long (Swanson et al., 2011). Disturbance events caused by insects provide numerous biological legacies: (1) remaining living trees, depending on previous stand characteristics; (2) rapid creation of dead wood, with abundant snags in the early stages and many fallen logs in later stages; and (3) understorey vegetation that remains undisturbed. The opening of the canopy dramatically alters microclimate conditions by, for example, warming soils, accelerating dead wood inputs, and releasing near-ground vegetation from overstorey competition (Forrester et al., 2012). The combination of biological legacies and canopy opening in disturbed stands may enhance biodiversity by allowing species to persist in disturbed areas, by modifying or stabilising environmental conditions in recovering stands, by providing essential habitats and sources of energy for a wider array of organisms, and by influencing recolonisation patterns (Lindenmayer & Franklin, 2002). The diversity of early successional stands is determined by the survivors of dense forests, plus the opportunists, pioneers and habitat specialists that depend on a high amount of dead wood (Swanson et al., 2011). Even food web diversity increases in early successional stands, and the recharging of nutrient pools is a dominant ecological process (Swanson et al., 2011).

The view that areas protected to conserve biodiversity should not be managed after disturbance to avoid removing biological legacies is not new and has been recommended several times (Noss et al., 2006; Swanson et al., 2011). For example, earlier studies have demonstrated the high biodiversity-enhancing effects of bark beetle infestation on species directly related to the bark beetle (Weslien, 1992) or to the open conditions created by the beetles (Burton, 2008; Müller et al., 2008). The broad ecological effects of windthrow on insect biodiversity also have been reported (Bouget & Duelli, 2004). However, non-intervention policies for large protected areas are still controversial for several reasons. First, conservationists fear the loss of mature and dense forested habitats in such areas, which in turn may negatively affect species dependent on mature stands (Koprowski et al., 2005). Second, nearby landowners fear the spread of beetles into commercial forests (McFarlane & Witson, 2008). Third, opportunities for recovering economic value through the sale of timber remain a consideration for management decisions in parks and protected areas that have modest funding, with such economic issues still often prompting intense discussion regarding "benign neglect" strategies in such areas (Müller & Job, 2009; Stokstad, 2006). Finally, the culture of foresters and land managers in general still tends to equate forest health with tree health (Edmonds et al., 2011).

Natural disturbances and forest management actions usually have distinctly different ecological effects, although both may cause similar changes in canopy structure (Niemela, 1999). As mentioned above, several previous studies have provided results on the biodiversity-enhancing effect of natural disturbance events. However, the narrow taxonomic scope in most of these studies, often with an emphasis on birds or one group of insects (Bouget & Duelli, 2004; Swanson et al., 2011) limits the interpretation of how generalisable such trends are for biodiversity as a whole (Gruppe, 2009). In the study presented here, the response of 24 lineages following a wave of bark beetle infestations in the non-intervention area of the Bavarian Forest National Park provides insight into the effects of recent and future disturbance events in conifer-dominated protected ecosystems in Europe.

Our study had two aims: first, to describe the development of the area opened by bark beetles in a mixed montane national park under a benign neglect strategy; and, secondly to assess the number of species associated with the different levels of canopy openness following the disturbance. We estimated the species preferring open, semi-dense and dense forests across 24 lineages from three kingdoms (plants, fungi and animals) to provide an objective view of the winners and losers of the disturbance event.

Materials and methods

Study area

Our study area was the Bavarian Forest National Park (~24,000 ha) located in south-east Germany, which covers an altitudinal gradient from 650 m to 1400 m a.s.l. Depending on altitude, the mean annual temperature (1972–2001) varies from 3.5 to 7.0 °C, and the total annual precipitation varies from 1300 to 1900 mm. Above about 1100–1200 m a.s.l., the high montane forest is dominated by Norway Spruce (*Picea abies*), with a low proportion of Mountain Ash (*Sorbus aucuparia* L.); below this altitude, the mixed montane forest is dominated by spruce, Beech (*Fagus sylvatica* L.) and Silver Fir (*Abies alba* Mill.). The national park was established in 1970 (~13,500 ha, described as the "old park" in this study; Fig. 1) and was extended in 1997 by ~10,500 ha (termed the "new part"), together forming the "current park". Most parts of the core zone with no management interventions (~10,000 ha) were established in the old park; the new part is still managed to prevent bark beetle outbreaks because of political constraints (Fig. 1). Since the late 1980s, several windthrow events and (especially) bark beetle infestations have considerably influenced the structural

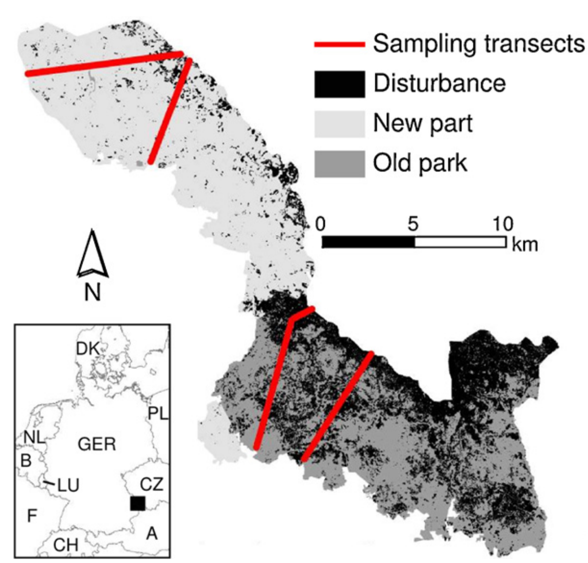

Fig. 1. Map of the Bavarian Forest National Park in 2009. The southern part ("old park") has been under protection since the 1970s. The northern part was added when the park was enlarged in 1997 (referred to as the "new part", which together with the "old park" forms the "current park"). Red lines show the location of plots sampled along four transects. The area of forest disturbed by windthrow or bark beetles from 1988 to 2009 is shown in black; for the development of the bark beetle infestation, see Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

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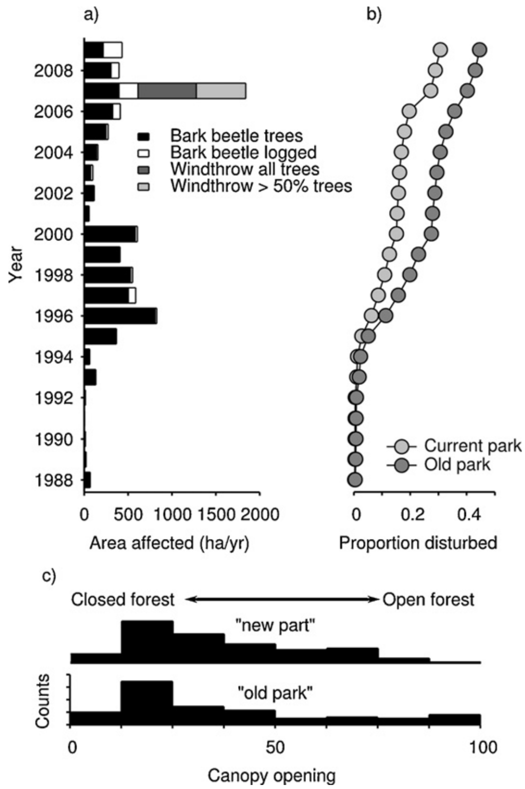

Fig. 2. (a) The area annually affected by bark beetle and windthrow in the Bavarian Forest National Park since 1988. (b) Cumulative percent of forest area affected by bark beetle and windthrow for the older part of the national park ("old park") and the "current park" (old park plus new part). (c) Histograms of the penetration rate in the non-intervention area of the old park and the new area representing mainly an ordinary commercial forest based on 288 plots (1 ha).

characteristics of the core zone. The history of natural disturbances, with areas calculated from yearly measurements of high-resolution aerial photos is summarised in Fig. 2a. In recent years, the infestation in the old park area decelerated, possibly because mature spruce stands are becoming scarcer.

Species data

We sampled species of 24 taxonomic groups: two plant lineages; two fungal groups; and, 20 animal lineages along four transects with a standardized procedure in the total park (Table 1). The number of sampled plots depended on the taxonomic group; for details of the conceptual framework, see Bässler et al. (2008). Briefly, the minimum distance between two sample plots of the same transect was 100 m. Flowering plants, ferns and wood-inhabiting fungi were sampled in a single survey from August to October 2006. All other taxa were sampled and trapped from 2006 to 2007. The presence of bats was recorded in 2009 with batcorders. For details of the specific methods for the groups under study, see Moning et al. (2009), Müller et al. (2009a, 2009b, 2012), Müller and Brandl (2009), Bässler et al. (2010), Raabe et al. (2010), and Vierling et al. (2011). Altogether, our data set comprised 2738 species. Because ecosystem requirements of very rare species cannot be adequately assessed with our approach, all species occurring in less than three plots were removed. The remaining data set contained 1542 species used in the final analysis.

Canopy opening by disturbance

As a direct measurement of the changes in habitat structure caused by the bark beetle infestations, the canopy penetration density was calculated using airborne laser scanning (Vierling et al., 2008). As a surrogate for radiation penetration rate or canopy openness we used the data from LiDAR (Light Detection And Ranging) beams reflected 2 m above ground divided by those reflected 50 m above-ground. The reflectance was gathered with airborne LiDAR techniques in May 2007 after annual leaf-out. Thus, forest canopy characterisation by LiDAR, with a point density of 25 laser shots per m^2, was conducted during the sampling of all animal groups except bats. However, the canopy of plots in which bats where sampled was not affected by disturbance between LiDAR acquisition in 2007 and bat sampling in 2009, likewise, no major changes in canopy structure occurred during winter 2006/07 between plant and fungi sampling and LiDAR acquisition. From these raw data, the mean penetration rate for a circular area of 1 ha and 0.1 ha around

Table 1
Summary of the taxonomic groups sampled, associated methodologies, data structure, overall species richness and organism abundance encountered. Results refer only to individuals identified to the species level.

Taxon	Number of plots	Sampling method	Data	Number of species	Number of individuals
Bryophyta	105	Mapping	Presence/absence	112	–
Eumycophyta	286	Mapping	Presence/absence	254	–
Lichenes	109	Mapping	Presence/absence	155	–
Spermatophyta	172	Mapping	Presence/absence	155	–
Mollusca	105	Pitfall traps	Abundance	46	3145
Lumbricidae	49	Soil extraction	Abundance	8	139
Opiliones	172	Pitfall traps	Abundance	9	1555
Araneae	36	Pitfall traps	Abundance	155	7855
Coleoptera	172	Flight-interception, pitfall, and malaise traps	Abundance	894	80,855
Collembola	172	Pitfall traps	Abundance	33	12,432
Isopoda	172	Pitfall traps	Abundance	10	216
Diplopoda	172	Pitfall traps	Abundance	9	89
Chilopoda	172	Pitfall traps	Abundance	11	216
Auchenorrhyncha	36	Malaise traps	Abundance	84	3078
Heteroptera	36	Malaise traps	Abundance	86	650
Lepidoptera	36	Light traps	Abundance	365	2222
Neuroptera	36	Malaise traps	Abundance	25	145
Syrphidae	36	Malaise traps	Abuncance	36	1716
Aculeata without Formicidae	36	Malaise traps	Abundance	108	1480
Formicidae	172	Pitfall traps	Abundance	15	19,151
Symphyta	36	Malaise traps	Abundance	82	904
Small mammals	172	Pitfall traps	Abundance	7	540
Chiroptera	32	Batcorder	Activity	14	10,577
Aves	172	Grid mapping	Abundance	65	5597

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each sampling site was derived (for details, see Müller et al., 2009b; Vierling et al., 2011).

Statistical analyses

The species typical of the different stages of forest stand development (i.e., characterised by canopy thinning and hence different canopy classes) were determined using indicator species analysis (Dufrêne & Legendre, 1997) using the "labdsv" module (Roberts, 2010) in R 2.12.0. This approach calculates an index (*IndVal*) that clearly measures the fidelity of a taxon to a specific range of an environmental factor or gradient.

Sampling sites were classified into three forest canopy classes (closed, transitional and open forest) according to radiation penetration rates. To test the robustness of the results of indicator species analysis, two modes were used for the classification. The first were equidistant classes: a closed canopy class characterised by 0 to <33% radiation penetration, a transitional class with 33 to <66% penetration, and an open canopy class with 66–100%. Class limits in the second mode were derived from the histogram of radiation penetration rates. Based on results of previous analyses and because approximately one-half of the sampling sites not infested by the bark beetle had radiation penetration rates between 0 and 15%, the closed canopy class limit was set to 15% radiation penetration. Because 75% of all sites affected by bark beetles had radiation penetration rates >50%, 50% was used as the break between the transitional canopy class and the open canopy class. For each species, the indicator values for the three forest canopy classes in both modes were calculated. The number of significant indicator species for each taxon and canopy class was counted using 10,000 permutations.

The relative frequency of individuals belonging to indicator species was calculated for each site. For taxa providing only presence/absence data, the number of indicator species in relation to all species of a site was calculated; these two values are referred to as relative abundances. To obtain the distribution of the relative abundances over all sampling sites, the sampling sites were sorted according to the radiation penetration rate, and a moving window with ten sampling sites was used; this window was shifted by one sampling site for the next calculation step. Relative abundances were then calculated for the ten plots in each window. A window size of ten sampling sites was used to reduce the variance originating from sampling sites with remarkably high or low abundances of indicator species owing to reasons other than the canopy penetration rate.

Results

The area affected by bark beetles in the Bavarian Forest National Park was bimodally distributed over time. After a rapid increase from 1995 onwards, the area affected remained high until a sharp decrease in 2001 (Fig. 2a). The affected area increased again starting in 2005 and continued to increase through the last sampling year, 2009. When we quantified the magnitude of the affected area within both the old and current national park, the total proportion of park area affected was clearly below 50% (Fig. 2b). Thus, both dense and open stands are well represented within the whole area of the national park. This finding was also supported when we compared the penetration rate in the areas occurring along the gradient of openness between the old park (subject to no intervention) and the new part (managed much like commercial forests) (Fig. 2c). Only the old park area strongly affected by bark beetle infestation had plots with a very open canopy. Because forest stands in the old park have not been thinned, very dense plots also were slightly more frequent in the old park than in the new one. Overall, the forest stands were more equally distributed along the gradient of canopy density in the old park than in the new area (Fig. 2c).

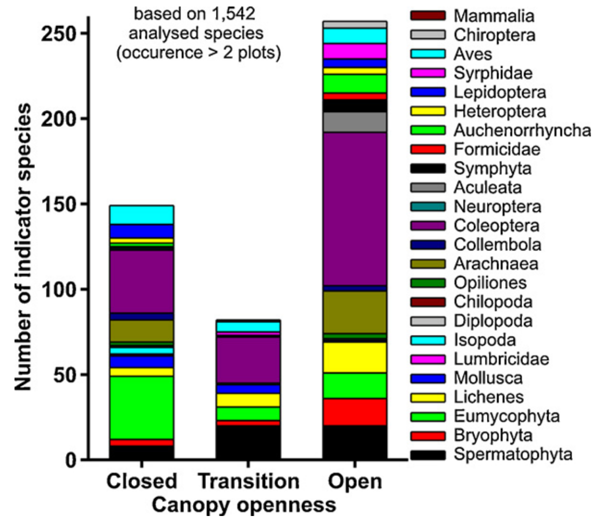

Fig. 3. Number of indicator species with a preference for closed forest, open forest, and those transitional between closed and open forests. Forest canopy openness was determined by measuring the radiation penetration rate in an area of 1.0 ha around the sample sites. The forest canopy class breaks were set at 15% and 50% radiation penetration.

We identified species with a preference for one of three classes of canopy openness (closed, transitional class, and open forest, as classified by radiation penetration rate), in areas of 0.1 ha and 1.0 ha around each sampling site. The results obtained for the two sizes of reference area and with both classification modes were very similar (not shown); therefore, we only present the results for the area of 1.0 ha, with forest canopy class breaks at 15% and 50% penetration. Out of the 1542 species analysed, 488 (31%) were significant indicator species (significance level: 0.05). Most of the significant indicator species (257) had a preference for open forest (Fig. 3). Approximately half of that number (149 indicator species) had a preference for closed forest. The lowest number of indicator species (82) preferred stands in the transitional canopy class (Fig. 3).

The species lineage distributions formed four patterns within the canopy openness classes. First, the number of indicator species of the taxa Arachnaea, Bryophyta, Coleoptera, Lichenes, Spermatophyta and Auchenorrhyncha was lower in closed forests than in open forests (Fig. 3). Second, the number of indicator species of the taxa Eumycophyta, Heteroptera, Lepidoptera and Mollusca in particular was higher in closed forests than in open forests. Third, the distribution of indicator species of some taxa indicated a preference for one end of the canopy density gradient because indicator species were missing at the other end; species of the taxa Aculeata (only bees and wasps), Formicidae, Symphyta and Chiroptera clearly preferred open forests, and species of the Isopoda preferred closed forests. Fourth, the number of indicator species of Collembola, Neuroptera and Mammalia did not show a clear preference as a group for any canopy openness class.

The relative abundance of indicator species from 12 selected lineages with a sufficient number of species calculated with a window of ten sampling sites across the gradient of radiation penetration is illustrated in Fig. 4. For most taxa, the distribution of abundance followed their preference for canopy openness. The distribution of abundance of indicator species in the closed forest class was as expected. However, Mollusca indicator species, most of which preferred the closed forest, were quite abundant in both open and closed forests. The species of Aves that preferred one class of canopy openness were also found in the other two classes. Only within the Lichenes and Spermatophyta were transitional

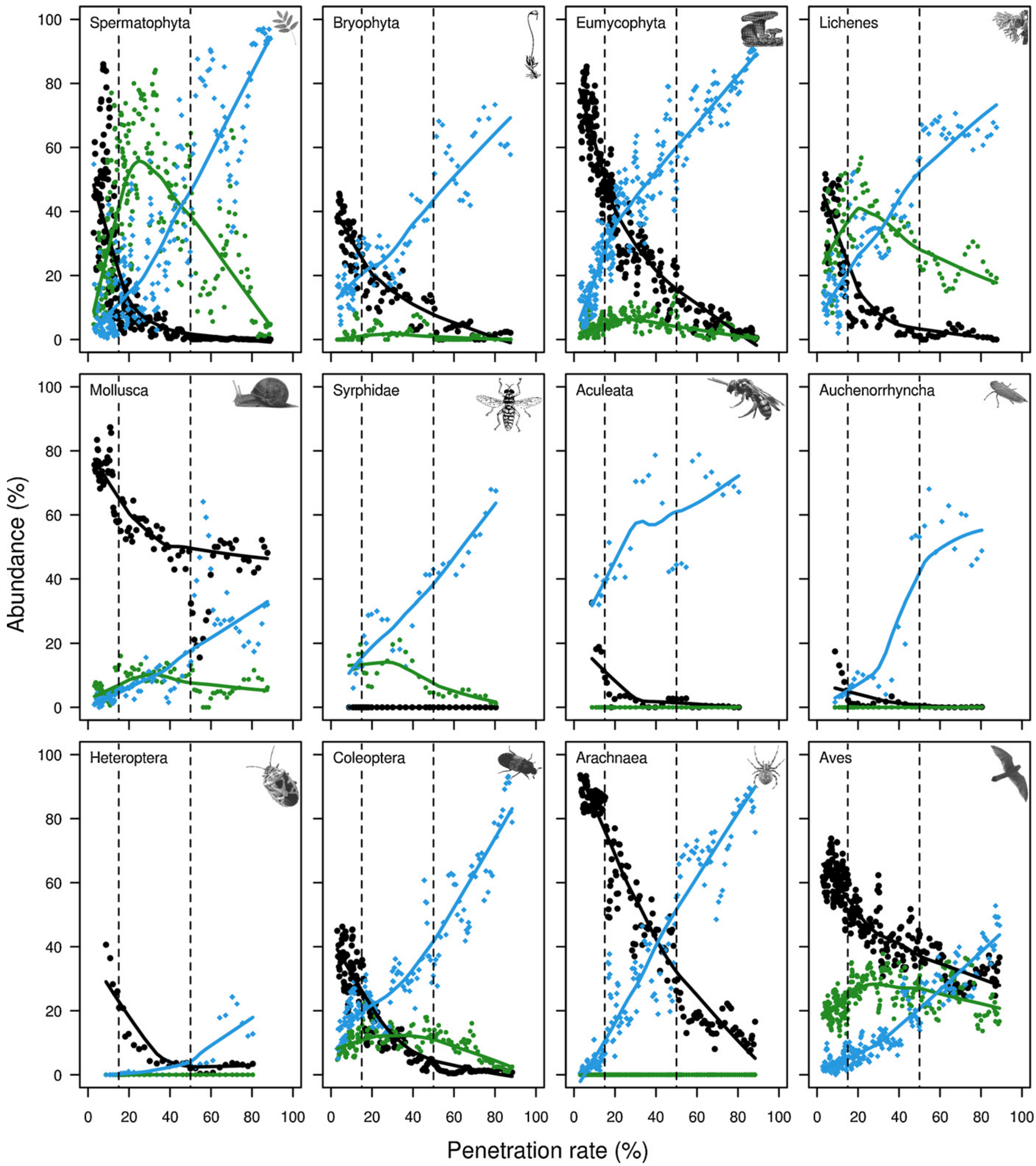

Fig. 4. Relative abundances of indicator species of 12 selected lineages in the three canopy openness classes in relation to the radiation penetration rate – black: indicator species preferring closed forest; green: indicator species preferring transitional forest; blue: indicator species preferring open forest. Relative abundances were calculated with a moving window of 10 sampling sites. The radiation penetration rate in an area of 1.0 ha around each sampling site was averaged over the window. From left to right and top to bottom, separate panels are presented for Spermatophyta, Bryophyta, Eumycophyta, Lichenes, Mollusca, Syrphidae, Aculeata without Formicidae, Auchenorrhyncha, Heteroptera, Coleoptera, Arachnaea and Aves. Canopy openness class breaks at 15 and 50% radiation penetration are indicated by the dashed vertical lines.

zone indicators more abundant in the transitional zone than in the other two canopy classes.

Discussion

Our study provides the first, broad, cross-taxonomic, aboveground estimation of the effect on species diversity of canopy opening caused by bark beetle disturbance. The methodology used in our study proved to be very robust when we varied the range of the classes of canopy openness or the spatial scale of the study plots and thus can be considered to provide very reliable results.

We found that almost twice the number of indicator species prefer open forests over closed forests, which supports the general view of Swanson et al. (2011) that naturally disturbed, early successional ecosystems provide an under-appreciated value for biodiversity conservation, and supports findings of previous studies that focused only on selected groups such as the Aculeata (Bouget & Duelli, 2004; Müller et al., 2008). However, our analyses facilitated a more differentiated picture, also revealing taxa with a clear preference for closed stands (e.g., Mollusca, Eumycophyta, Lepidoptera). We therefore conclude that biological legacies are not only important in open stands after a natural disturbance but also that biological legacies such as dead wood play a key role under a dense canopy. However, since only two taxa (Eumycophyta and Coleoptera) are considerably linked to the amount of dead wood, this is not the main driver of our indicator species analysis results. The number of indicators of the Eumycophyta was even higher in the closed forest cluster than under open canopies. The saproxylic beetles (280 of 894 analysed beetle species) in the area of investigation are known to depend both on the amount of dead wood and on canopy structure (Müller et al., 2010). Thus, our results demonstrate that both open and closed forests are important for sustaining diversity in a temperate mixed montane forest.

One of the taxa with many species negatively affected by the openness of the canopy was the Mollusca. One reason for this finding is most likely the decreasing moisture with increasing canopy openness (Kappes, 2005). Several of these species are known to be dependent on long-lasting, stable microclimatic conditions in temperate broadleaf forests (see discussion in Moning & Müller, 2009). However, the presence of some Mollusca indicator species in open forests as well as in the transitional class between open and closed forests indicated a lower degree of preference of the complete taxonomic group. Therefore, the species composition of molluscs in open and dense forests can be considerably different. Similar patterns have also been demonstrated for saproxylic beetles, with a preference of dead wood associated beetles for sun-exposed open forest stands and fungus feeders for closed forests (Müller et al., 2010) and for the diversity of Eumycophyta (Bässler et al., 2010).

The highest number of indicator species with a preference for open forest stands was of the taxa Aculeata and Formicidae. The canopy structure is the most important factor for predatory wasps of the Aculeata, but not for the bee species on which they prey, which may be more closely linked to the tree and understorey plant diversity (Fye, 1972; Sobek et al., 2009). Such a higher diversity of plant species on open forest sites has been shown in previous studies on the Czech side of the Bohemian Forest (Jonášová & Prach, 2008). The preference of the Formicidae for open forest can be explained by the higher ground temperature in open forests, as shown by Kumischick et al. (2009). The third taxon preferring mainly open forests is the sawflies (Hymenoptera: Symphyta; Flückiger, 1999). Here, the composition of plant species and favourable, warm microhabitat conditions may be more important factors than canopy structure for suitable larval habitats. Gossner et al. (2007) have already reported a low number of sawfly species on *Picea abies*, which is the predominant tree species affected by *Ips typographus* in the area under investigation. Therefore, the lack of trees suitable for feeding by sawflies in the closed forest cluster may also be the reason for the absence of this group of indicator species in the closed forest. The general preference for open habitats by many Coleoptera species has been outlined in several studies of our region and can be linked to species traits. In general, species of small body size increase in open stands (Müller & Brandl, 2009). Even though the Araneae showed preferences similar to those of the Coleoptera, the number of species indicators in the transitional canopy class was considerably lower. This is in keeping with the results of other studies, which outlined strong differences in spider species composition between open areas and closed spruce forest (Matveinen-Huju et al., 2009; Pearce et al., 2005; Vierling et al., 2011).

The typical stages of post-disturbance stand recovery and succession in spruce stands attacked by bark beetles and the dominant species of those stages have been investigated in several studies (Kupferschmid & Bugmann, 2005). According to Jonášová and Prach (2008), the forest herb layer and the bryophyte cover survive significantly more frequently in stands affected by the bark beetle than in logged areas. Therefore, the number of pioneer plant species colonising bark-beetle-infested stands is lower. The number of Aves indicator species was similar in all canopy classes, probably because temperate bird assemblages are more closely linked to vegetation structure than to plant species composition (MacArthur & MacArthur, 1961) and because bird species of open stands in montane forests form distinct communities (Moning & Müller, 2008).

Our finding that the transitional class between closed and open forests had the lowest number of indicator species has an important implication for management strategies not only in protected forests. Commercial forestry in most of Europe reduces the overall period of canopy closure by a combination of thinning and final harvests. Furthermore, it avoids open forests by rapid planting after clear-cuts and disturbances. Both practices lead to a shorter gradient of canopy density in managed forests than in natural forests, which have a more patchy structure. This is also supported by Fig. 2c, with a more equal distribution of different canopy density conditions after disturbance (old park) compared to managed forests (new park). The expansion of the gradient in canopy openness by increasing very closed and opened stands provided broader habitat patchiness on the landscape scale. The fact that disturbances such as stand-replacing fires may provide greater heterogeneity at the landscape level was also one key result from studies after the large fire in Yellowstone National Park (Turner et al., 2003). The investigation of plant diversity patterns there illustrated the opposite of the widely-held fear that such a large disturbance homogenises the landscape. The analysis of satellite imagery after wildfires in Canada's boreal forest likewise confirms that natural disturbances are agents of habitat diversification (Burton et al., 2008).

However, we will not deny that in certain situations, a disturbance affecting a small isolated population in a mature coniferous forest can result in the local extirpation of a species. Such a negative impact of large-scale canopy opening by bark beetles threatened an endemic squirrel in Arizona (Koprowski et al., 2005). In our area, one such possibly sensitive species is the Capercaillie, *Tetrao urogallus* L., a species of mature spruce forests. Interestingly, the species did not disappear from stands characterised by large areas of standing dead wood (Teuscher et al., 2011). On the landscape scale, the Capercaillie population seemed to be enhanced by the increase in patchiness of open and closed stands. For this species, long-lasting early successional stages would probably be the most advantageous, as predicted by Swanson et al. (2011).

In answer to the question of how large a protected area should be, the usual response is "more is better". To this end, the national

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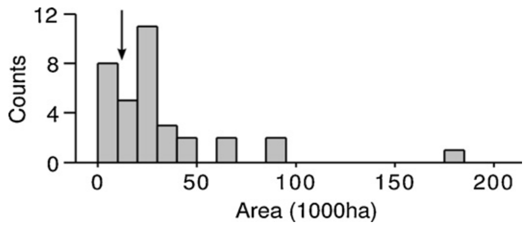

Fig. 5. Histogram portraying the frequency of national parks in mountain areas of Central Europe with conifers according to their area. The arrow indicates 10,000 ha, which should be sufficient for sustaining high habitat heterogeneity even with heavy levels of natural disturbance.

park that constitutes our study area was enlarged to improve its value as a protected area. Our case study demonstrated that the older park of ~13,500 ha was large enough to ensure that the entire gradient of canopy openness is present even after large-scale disturbances (Fig. 2b). Most national parks in the mountains of Europe are, in fact, larger than 10,000 ha (Fig. 5). In those larger protected areas, natural disturbances play an important role in naturalising or restoring anthropogenically impacted forest landscapes. However, beyond these protected areas, biological legacies present after disturbances can also play an important role in conserving biodiversity in managed landscapes. The retention or re-introduction of dead and damaged trees, and the protection of naturally disturbed forests from reactive salvage logging, is being advocated in western North America and Australia as well as Europe (Bauhus et al., 2009; Burton, 2010; Lindenmayer et al., 2008).

Implications for management

The Bavarian Forest National Park experienced a large-scale bark beetle outbreak, which is almost at its end in the older part of the park. The broad taxonomical indicator species approach led to the general implication that early successional ecosystems after bark beetle infestation provide some of the most species-rich natural habitats in the montane forests of Central Europe. The ecological explanation for this high diversity is likely a combination of biological legacies, pioneer species, opportunists and habitat specialists. The finding that closed and open forests with high amounts of dead wood both provide important habitats for species with apparently contrasting requirements implies that management for biodiversity should promote extremes of canopy openness in a patchy landscape. For national parks in the mountains of Central Europe dominated by conifers (~70% *Picea abies* and *Pinus sylvatica*, but admixed with broadleaf trees or *Abies alba*), with an active disturbance regime of fire, insects and windthrow, our case study supports the view that unmanaged core zones of ~10,000 ha are sufficient to sustain the whole set of biological legacies of dense and early successional forests, without a loss of species adapted to any one stage. Our results further indicate that so-called "damaged" forests provide high conservation value.

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