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Forest restoration as a double-edged sword: the conflict between biodiversity conservation and pest control

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SUMMARY

1. Forestry has markedly changed a large proportion of the world's boreal forests, often with negative effects on biodiversity. As a result, forest restoration is increasingly implemented to counteract the negative effects. However, restoration measures aimed at mimicking natural disturbance regimes could simultaneously increase the risk of unwanted negative effects, such as damage by forest pest species. This study compares the effect of two restoration methods (prescribed burning and gap-cutting), on both biodiversity conservation and pest control, to provide a basis for solutions to this potential conflict.

2. Bark beetles are ideal for studying this conflict, as this group is both species-rich and contains notorious pest species. We conducted a unique, large-scale field experiment in which we compared the effect of two different restoration methods on the abundance, species richness and assemblage composition of bark beetles. In addition, we estimated uncontrolled tree mortality by the number of trees that died post-restoration.

3. Beetles were divided in two groups, primary and secondary, the former with an ability to kill growing trees. Bark beetle diversity did not differ between treatment groups prior to restoration. However, after restoration, assemblage composition and primary bark beetle abundance differed between the treatments. Furthermore, species richness was higher in burned and gap-cut stands compared to reference stands.

4. The number of trees that died post-restoration was highest on burned sites, whereas no difference was found between gap-cut and reference stands. The number of dead trees was correlated with the number of primary beetles.

5. *Synthesis and applications*. We demonstrate the potential for a conflict between forest restoration for biodiversity conservation and the potential risk for tree mortality caused by forest pests. This is likely to become a problem in many boreal forests; however, our results suggest that this conflict can be moderated by the choice of restoration method. The restoration method gap-cutting had a similar positive impact on bark beetle species richness as compared to the burning method, but did not as burning, increase tree mortality. Thus, in areas where there is an apparent risk for pest outbreaks, our data suggest that gap-cutting should be the chosen method to avoid an unwanted increase in tree mortality at the stand level.

Key-words: abundance, assemblage composition, bark beetles, dead wood, forest restoration, pest control, *Pityogenes chalcographus*, *Polygraphus poligraphus*, prescribed burnings, species richness

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Introduction

Intensive extraction of natural resources has led to changes in ecosystem structures and processes, losses of biodiversity and declines in ecosystem services (FAO 2010). As a result, ecological restoration with the aim of increasing biodiversity is recognized as a global priority (Jacobs *et al.* 2015; Stanturf 2015). As restoration measures have the potential to affect entire ecosystems with many interacting species, it is likely that such measures designed to affect threatened species positively, may at the same time, cause damage such as fire or flooding, or may promote invasive species (Buckley & Crone 2008). In forests, restoration measures may increase dispersal and elevate risks of pest species outbreaks (Toivanen, Liikanen & Kotiaho 2009). This potential conflict has seldom been studied empirically.

Forestry has markedly changed significant proportions of boreal forest ecosystems during the last century (Esseen *et al.* 1997; Brassard & Chen 2006; Potapov *et al.* 2008; Paillet *et al.* 2010; Bernes 2011), with negative effects on biodiversity (Butchart *et al.* 2010; Paillet *et al.* 2010). The main reasons are habitat loss, forest fragmentation, simplified forest structure and reduction in dead wood. In addition, fire control has resulted in reductions in fire frequency in many boreal forests of, for example, Europe (Granström 2001) and North America (Cumming 2005). Many forest species dependent on dead wood and burned forests are therefore threatened (Tikkanen *et al.* 2006). As the exploitation of boreal forest is continuing (Potapov *et al.* 2008), we need to find ways to mitigate these negative effects on biodiversity. Consequently, restoration of degraded forest stands is being undertaken world-wide. This study is based on restoration theory that builds on the assumption that mimicking natural processes and disturbances and ideally the restoration of disturbance sources, is an efficient way to promote biodiversity (Angelstam 1998; Kuuluvainen 2002; Lindenmayer, Franklin & Fischer 2006; Parker, Clancy & Mathiasen 2006; SER – Society for Ecological Restoration 2012). The structure and dynamics of boreal forests have historically been influenced by both stand-replacing disturbances, mainly initiated by fire and wind, and small-scale disturbances causing the death of individual trees (Niklasson & Granström 2000; Kuuluvainen 2002; Brassard & Chen 2006). Consequently, prescribed forest burning can be used as a measure to restore habitats for fire-adapted animals and plants at larger scales (Larsson & Danell 2001; Buddle *et al.* 2006; Kouki *et al.* 2012). Efforts to mimic natural small-scale stand dynamics in restoration include small-scale selective-cutting and different forms of dead wood creation (Kuuluvainen 2009; Djupström *et al.* 2012; Bell *et al.* 2015; Hägglund *et al.* 2015). Such restoration measures are frequently undertaken, particularly in the boreal forests of America (Keane *et al.* 2017) and Europe (Halme *et al.* 2013) and the world-wide interest in forest restoration is increasing considerably (Jacobs *et al.* 2015).

However, restoration measures that attempt to increase the amount of dead wood commonly generate conflicts between goals, such as biodiversity conservation and timber production (Gustafsson *et al.* 2012). An additional source of conflict could be that forest restoration involving dead wood creation increases population densities of primary bark beetles (Eriksson, Lilja & Roininen 2006; Johansson *et al.* 2006; Parker, Clancy & Mathiasen 2006; Campbell, Hanula & Outcalt 2008) that have the capacity to kill standing trees. The risk of bark beetle damage adjacent to restoration areas has previously been studied (Eriksson, Lilja & Roininen 2006; Komonen & Kouki 2008; Toivanen, Liikanen & Kotiaho 2009) but no studies have compared the effects of different restoration methods on biodiversity conservation and pest control, using large-scale long-term field experiments in an attempt to find solutions to the potential conflict.

Bark beetles (Scolytinae; Curculionidae; Coleoptera) are a group of insects that include species with large economic and ecological impacts, with the potential to affect whole ecosystems. For example, some species (*Scolytus* spp. and *Hylurgopinus rufipes* Eichhoff) transmit fungus causing the Dutch elm disease, which has killed large numbers of elms across Europe and America (Brasier & Buck 2001). In addition, more than 25 million hectares of pine forests were killed during the recent outbreak of *Dendroctonus ponderosae* Hopkins in western North America (USDA Forest Service, Forest Health Protection, and Natural Resources, Canada, Canadian Forest Service). Finally, the total forest area damaged by bark beetles (mainly *Ips typographus* L.) in Europe was estimated to be 145 million m^3 between 1950 and 2000 (Schelhaas, Nabuurs & Schuck 2003). The outbreak magnitude of many bark beetle species in boreal forests has increased in recent decades and it has been suggested that this is linked to climate change (Jönsson *et al.* 2007; Bentz *et al.* 2010).

Only a few bark beetle species are able to damage and kill living trees; the remainder (~7300 species, Stokland & Siitonen 2012) can be defined as secondary or saprophagous, with important ecological impacts as major decomposers of woody material. The number of bark beetle species in northern Europe is 102 (Stokland & Siitonen 2012), but only a handful are primary species with the ability to colonize living trees (Rudinsky 1962). The bark beetle species in Sweden and elsewhere are numerous and sometimes red-listed (Gärdenfors 2015) and the number of species is often positively correlated with the species richness of saproxylic beetles (e.g. Martikainen *et al.* 1999), which are commonly threatened in Fennoscandia (Jonsell, Weslien & Ehnström 1998; Tikkanen *et al.* 2006). Thus, bark beetles are a suitable group of insects for studying the possible conflict between biodiversity conservation and the risk of pest damage as a consequence of forest restoration measures. Here, we report how two forest restoration practices commonly used in Scandinavia affect this group of forest insects.

The two types of forest restoration measures – prescribed burning and gap-cutting – studied here were chosen as they are expected to affect the bark beetle community and are intended to mimic natural disturbances. The objective is to evaluate the effect of forest restoration on: (i) biodiversity (in this study defined as bark beetle species richness, abundance and assemblage composition as a proxy), (ii) the abundance of primary bark beetles (potential pest species), and (iii) tree mortality potentially caused by primary bark beetles. To our knowledge, this is the first time a large-scale field experiment has been used to provide a basis for finding solutions to the potential conflict between biodiversity conservation and pest control.

Materials and methods

The field experiment was conducted in 18 forest stands in northern Sweden during the years 2010–2015 and included (i) six prescribed burnings, (ii) six gap-cut stands and (iii) six reference stands (untreated controls). All types of stand were equally distributed across the study area (Fig. 1), they were representative of the types of mature, managed stands found in northern Sweden based on age, standing volume, tree species and dead wood (Table 1; Hägglund *et al.* 2015). Of the dead wood in the three prospective restoration sites, fallen trees accounted for between 49% and 53%. The corresponding percentages of dead spruce *Picea abies* (L.) and dead pine *Pinus sylvestris* L. were 11–16% and 13–23% respectively. Field layer vegetation of *Vaccinium myrtillus* L. or *V. myrtillus – Vaccinium vitis-idaea* L. – was dominant at all sites.

Immediately after the restoration treatment, prescribed burning had created higher volumes of dead wood in comparison to reference stands, but not in comparison to gap-cuts (Hägglund *et al.* 2015). Gap-cut stands differed from reference stands with respect to restoration-created dead wood. The prescribed burnings were conducted between 10 June and 3 August 2011 (the difference in timing was due to variations in suitable conditions for burning during the growing season), whereas the artificial gap-cuts were created in the winter/spring of 2011, well before insect flight periods. For the stands with gap-cuts, six gaps per hectare were created**,** covering 19% of each forest stand. The volume of dead wood per ha created in the burned and gap-cut stands varied between 9·1 and 69·4 m^3 ha^{-1} (41·7 ± 20·9 SD) and 15·5 and 23·9 m^3 ha^{-1} (20·1 ± 3·3 SD) respectively.

Table 1. Structural characteristics of the experimental forest stands prior to restoration. Sample mean ± SD. Ranges represent the variations found in all treatment groups

Treatment	Burned	Gap-cut	Reference	Range
Total volume (m^3 ha^{-1})	225·2 ± 34·3	222·3 ± 31·7	203·5 ± 27·8	150–270
Scots pine vol. (%)	58·3 ± 13·3	53·3 ± 15·1	51·7 ± 13·3	30–70
Norway spruce vol. (%)	31·7 ± 9·8	40·0 ± 14·1	33·3 ± 15·1	30–60
Deciduous vol. (%)	10·0 ± 6·3	6·7 ± 5·2	15·0 ± 5·5	5–20
Dead wood (m^3 ha^{-1})	12·8 ± 4·0	12·1 ± 1·9	10·2 ± 2·0	3–26
Stand age	118·0 ± 30·5	119·0 ± 22·8	110·7 ± 33·1	80–160

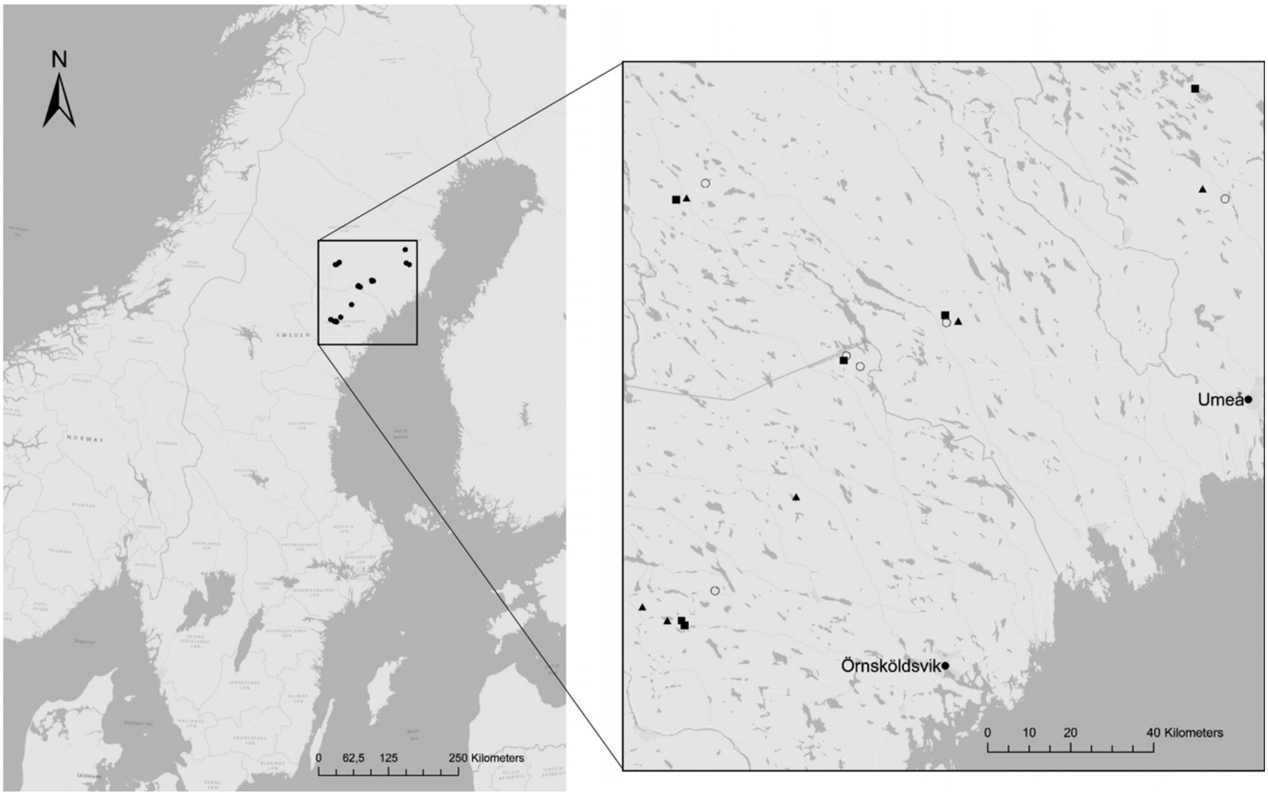

Fig. 1. Locations of the 18 study sites of burned (filled squares), gap-cut (open circles) and reference sites (filled triangles) in the north-east of Sweden.

The stands were voluntary set-asides for biodiversity (for approved FSC-certification) and were selected based on stand data provided by the forest company Holmen and visual inspection of them all. Forest stand size varied between 3·5 and 21 ha and they were dominated by *Pin. sylvestris* and *Pic. abies* L. Karst, with some deciduous trees such as *Betula pendula* Roth, *Betula pubescens* Ehrh., *Populus tremula* L. and *Salix caprea* L.

More detailed information about the study sites and treatments can be found in Hägglund *et al.* (2015).

TRAP CATCHES

To collect bark beetles, three flight-intercept traps (Polish IBL2 model – for detailed description see Pettersson *et al.* 2007) per forest stand (18) were placed at a height of 1–2 m from the ground, separated from each other by c. 50 m and at a distance of c. 30 m from the stand centre with a between-trap angle of 120°. Trapping was conducted during three consecutive years: 2010 (pre-restoration) and 2011 and 2012 (post-restoration). In 2011, 2 days after each prescribed burning, traps were placed out in the burned stand and in one paired gap-cut and one reference stand. This means that the start of the trapping ranged from early June until early August in 2011. In 2012, all traps were placed out in early June, that is, before the main flight periods for the majority of the beetles. The traps were emptied in September each year. All bark beetles were counted and identified to species by taxonomic experts.

TREE MORTALITY AND BARK BEETLE COLONIZATION

To evaluate whether restoration influenced the risk of tree mortality and colonization by bark beetles, trees that had died were surveyed at all study sites. Within transects permanently marked with tape (400 m × 10 m per site), all recently fallen and standing dead coniferous trees with a dbh >10 cm, were counted and marked in 2011 (pre-restoration/natural causes), 2012 (post-restoration/restoration causes) and in the autumn of 2015 (post-restoration/potentially caused by bark beetles). To determine bark beetle colonization (in 2015), all dead trees within the transects were checked for entrance and emergence holes to determine presence, and egg gallery pattern or adults from bark samples at a height of 1·3 m to identify beetle species. Where species was in doubt, bark samples were collected or photos of the galleries were taken for further identification in the laboratory.

STATISTICAL ANALYSES

The effects of forest restoration on bark beetle diversity and tree mortality were analysed using generalized linear models (GLM). Species richness, abundance and assemblage composition were analysed using data collected prior to restoration measures (from 1 year) and after restoration measures (pooled data from 2 years). Analyses of abundance were conducted on two different groups of data: (i) general bark beetles and (ii) primary bark beetles. The former included all species of bark beetles and for the latter, six species qualified as Primary: *I. typographus*, *Ips duplicatus* Sahlberg, *Pityogenes chalcographus* L., *Polygraphus poligraphus* L., *Polygraphus punctifrons* Thomson and *Polygraphus subopacus* Thomson (Rudinsky 1962). We consider all three *Polygraphus* species in the study to be primary, although the biological data pertaining to *Po. punctifrons* and *Po. subopacus* is quite scarce (Lekander 1959). The results did not change considerably by including or excluding these two species in the models, nor the correlation between beetle density and tree mortality. Considering differences in species richness, secondary and primary beetles were also analysed (GLM) for both years separately after restoration. Spatial variations were examined by including the coordinates as explanatory variables.

A fourth GLM model evaluated the differences in number of bark beetle-colonized trees between the treatments. Because the data pertaining to abundances and tree mortality varied too much to be adequately described by a Poisson distribution, we used quasi-Poisson distributions. Models of species richness were fitted using a Poisson distribution. *Post hoc* multiple comparisons among treatments were conducted with Tukey contrasts using the multcomp package (Hothorn, Bretz & Westfall 2007). To test for differences in bark beetle assemblage composition between treatment groups, we used Non-Metric Multidimensional Scaling from the vegan package (Oksanen *et al.* 2013) and manyglm from a GLM-based multivariate abundance package: mvabund (Wang *et al.* 2012). The manyglm data were best fitted using a negative binomial distribution. Adjusted *P*-values were calculated using 999 residual samples and an alpha set to 0·05. All data were analysed in R version 3.2.2 (R Development Core Team 2015).

Results

SPECIES RICHNESS AND ABUNDANCE

Before treatments, the recorded abundance (hereafter referred to as simply abundance) of bark beetles was 362, 520 and 584 (sum: 1466), and the recorded species richness (hereafter referred to as simply species richness) was 14, 16 and 14 in the prospective burned, gap-cut and reference sites respectively (Fig. 2a). There were no significant differences, either in abundances or species richness (Table 2). After treatment, a total of 6547 bark beetle individuals divided over 26 species were caught in the traps during the two study years. Of these 6547 individuals, 3482 (53%) were caught in the burned stands, 2171 (33%) in the gap-cuts and 894 (14%) in the reference sites (Fig. 2b). The number of species found in each treatment was 26 (100%), 21 (81%) and 13 (50%) respectively. None of the species recorded in this study were red-listed. Species richness and abundances in the burned stands were significantly higher than in the reference sites (Table 2). There was also a higher abundance and species richness in the gap-cuts compared to the reference stands. However, there was no difference either in abundance or species richness between burned stands and gap-cuts. In the restoration year (2011), only 14 of all the bark beetle species caught were found. The corresponding number in 2012 was 26. Species richness between 2011 and 2012 increased in all treatments with smaller changes for the reference stands (Fig. 3a). The opposite was true for the abundances of secondary bark beetles (Fig. 3b).

PRIMARY BARK BEETLES

Primary bark beetles, as a group, were significantly more abundant within the burned stands than in the gap-cut and the reference stands (Table 2; Fig. 4a), and this difference was mainly caused by the high numbers in 2011

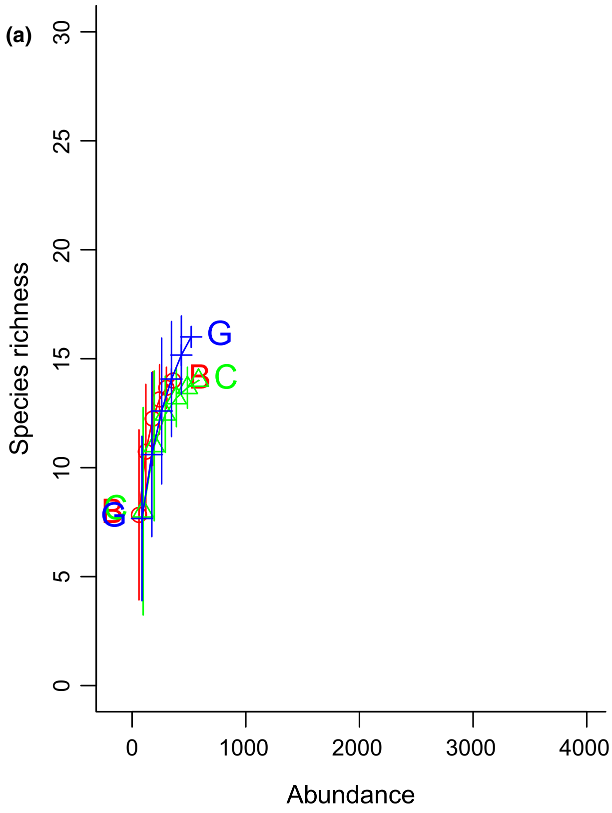

Fig. 2. Species accumulation curves, 1 year prior to restoration (a) and the sum of the 2 years after restoration (b) including all bark beetle species. The different forest restoration types were: burned (B, red, open circles) and gap-cut (G, blue, crosses), compared to the untreated reference stands (C, green, open triangles). The error bars indicate standard deviations from random permutations of the data. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 2. Outputs of the GLM models of recorded abundances and species richness of bark beetles in general and abundances of primary bark beetles, with data from traps prior to (pre-restoration) and after (post-restoration) treatments

	Abundance				Species richness	
	General†		Primary†		General‡	
Variables	Estimate	SE	Estimate	SE	Estimate	SE
Pre-restoration						
Intercept	12·748	21·978	−42·900	27·203	−3·836	15·714
Reference – burned	0·456	0·318	−0·303	0·380	0·0267	0·206
Gap-cut – burned	0·441	0·328	−0·497	0·415	−0·014	0·208
Gap-cut – reference	−0·015	0·294	−0·194	0·447	−0·017	0·393
N-coord	<0·001	<0·001	**<0·001****	<0·001	<0·001	<0·001
E-coord	<0·001	<0·001	**<−0·001***	<0·001	<0·001	<0·001
Post-restoration						
Intercept	**60·388***	22·421	**85·258*****	15·788	12·814	12·198
Reference – burned	**−1·413****	0·337	**−3·381*****	0·497	**−0·676*****	0·171
Gap-cut – burned	−0·415	0·250	**−1·354*****	0·229	−0·132	0·147
Gap-cut – reference	**0·997***	0·361	**2·027*****	0·532	**0·544****	0·178
N-coord	<0·001	<0·001	**<0·001****	<0·001	<0·001	<0·001
E-coord	<0·001	<0·001	<0·001	<0·001	<0·001	<0·001

†GLMs fitted using a quasi-Poisson distribution, due to overdispersion.
‡GLMs fitted using a Poisson distribution.
Significant values are shown in bold and indicated $*P < 0{\cdot}05$, $**P < 0{\cdot}01$ and $***P < 0{\cdot}001$.

(Fig. 3c). In contrast to the abundance of general bark beetle species, a significant difference was found between the gap-cut stands and the burned stands. The total abundance of primary bark beetles in burned, gap-cut and reference stands was 2458 (80%), 518 (17%) and 90 (3%) respectively. The number of primary bark beetle

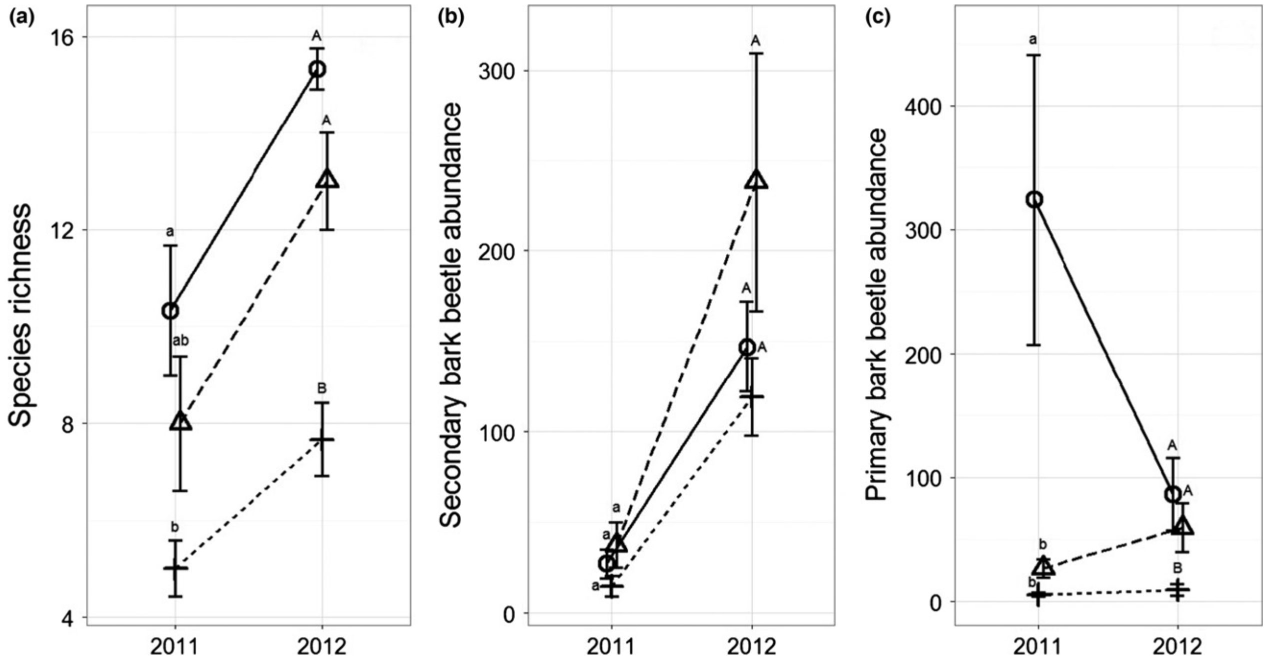

Fig. 3. Post-restoration temporal differences in average recorded species richness including all bark beetles (a), and average recorded abundances of secondary (b) and primary (c) bark beetles, under the different restoration measures. Burned stands are represented by open circles/solid line, gap-cuts by open triangles/long-dashed line and reference stands by crosses/dashed line. The error bars indicate standard errors. Different lower case letters and upper case letters indicate significant differences in 2011 and 2012 respectively.

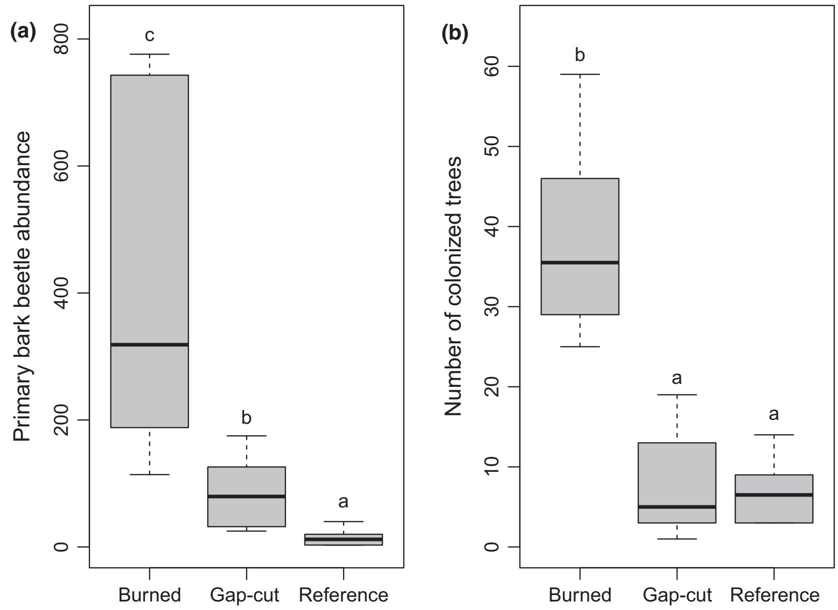

Fig. 4. (a) Recorded abundance of primary bark beetles (pooled from 2011 to 2012) evaluated from traps and (b) the recorded number of colonized trees (standing and wind felled from 2015) in different restoration treatments. Mean numbers are centred at in each box, whereas the lines represent the median. Box edges and error bars represent 25%, 75% quartiles and max and min values respectively.

species was, six, five and four. In the restoration year (2011), 83% of all bark beetles caught were primary species, with mean numbers of 324, 27 and 6 in the burned, gaps-cut and reference stands respectively (Fig. 3c). The corresponding values in 2012 were 28%, with mean numbers of individuals of 87, 60 and 9 individuals. The spatial effect of primary bark beetle abundances was limited, but significant (Table 2). The best fit was found in decreases from the south to the north.

There was a strong correlation between the number of post-restoration colonized trees found in 2015 and the number of primary bark beetles in the traps, pooled from 2011 and 2012 ($r = 0{\cdot}69$, $P = 0{\cdot}002$; Fig. 5). This was stronger than if all bark beetle species were included ($r = 0{\cdot}58$; $P = 0{\cdot}011$).

TREE MORTALITY AND BARK BEETLE COLONIZATION

In 2015, the total number of post-restoration dead trees recorded in transects was 318, with 230 (72%), 46 (15%) and 42 (13%), in the burned, gap-cut and reference stands respectively. Of these, 307 (97%) had signs of bark beetle

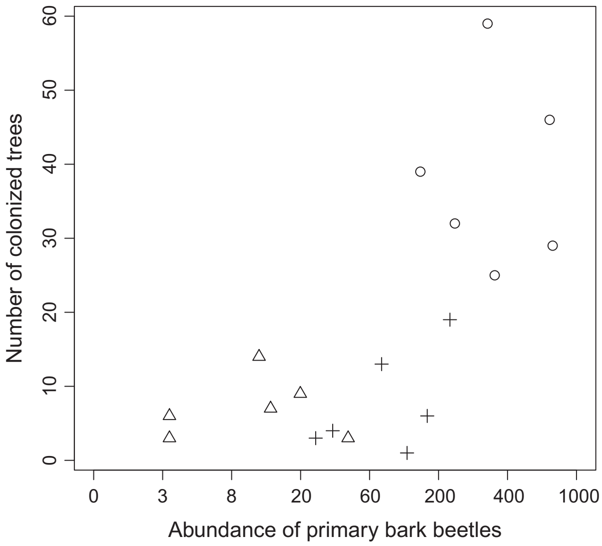

Fig. 5. Recorded abundance of bark beetles (log) from trap catches, and the correlation with recorded number of dead trees from the transects. Circles represent the burned stands, crosses the gap-cut stands and triangles the reference stands.

colonization and 27 (burned), 20 (gap-cut) and 21 (reference) were wind-felled. Of the colonized tree species, 70% were Norway spruce *Pic. abies* and 30% Scots pine *Pin. sylvestris*. There was no difference in percentages between the two tree species regarding standing and wind-felled trees**:** 80% standing and 20% wind-felled. The mean diameters (dbh: 1·3 m) of the dead spruces and pines ranged from 9·6–18·6 cm and 9·0–31·1 cm (burned), 11·3–24·0 cm and 16·8–28·9 cm (gap-cut) and 14·7–21·3 cm and 17·5–27·9 cm (reference) respectively. The number of dead trees was significantly higher in the burned stands than in the reference and gap-cut stands (Fig. 4b; Table 3). No difference was found between the gap-cut and reference stands. Primary bark beetles were observed in 78% of the dead trees. Of these, 72% were observed in the burned areas and 14% in both the gap-cuts and reference stands. Six additional wood-dwelling beetle species were identified in the colonized trees, that is, *Crypturgus pussilus* Gyll., *Dryocoetes autographus* Ratz., *Hylurgops palliatus* Gyll., *Pi. quadridens* Hartig., *Trypodendron lineatum* Oliver. and *Xylechinus pilosus* Ratz.

ASSEMBLAGE COMPOSITION

The bark beetle assemblage composition did not differ prior to restoration among the prospective treatment sites (Fig. 6a). However, after restoration, the bark beetle composition changed between reference and burned stands (Dev:139.7; $P < 0{\cdot}001$), gap-cut and burned stands (Dev:72.9; $P < 0{\cdot}05$) and gap-cut and reference stands (Dev:68.9; $P < 0{\cdot}05$) (Fig. 6b). The differences were strongly driven by the primary bark beetles. *Pityogenes chalcographus* and *Po. poligraphus* were approximately 50 times more abundant in burned stands and four species present in burned stands, *Hylastes brunneus* Erichson, *I. typographus***,** *Pityogenes bidentatus* and *Pi. quadridens*, were not present at all in the reference stands (Table S1, Supporting Information). In contrast, only one species contributed significantly to the differences in assemblage composition between burned and gap-cut (*Po. poligraphus*, more abundant in burned stands) and gap-cut and reference stands (*Pi. chalcographus* more abundant in gap-cut stands). The two other species of the genus *Pityogenes* (*Pi. bidentatus* and *Pi. quadridens*) and *H. brunneus* were many times more abundant in the burned sites compared to the reference stands. There were more *I. typographus* found in the burned compared to the reference stands, although the overall numbers of this species were generally low.

Table 3. Outputs of the main GLM and *post hoc* models (fitted using a quasi-Poisson distribution), regarding the number of bark beetle-colonized coniferous trees found in the transects. Significant values (P<0·05) are shown in bold

Tree mortality	Estimate	SE	t-value	P-value
Intercept	−20·072	19·568	−1·026	0·324
Reference – burned	−1·676	0·341	−4·909	**<0·001**
Gap-cut – burned	−1·599	0·329	−4·868	**<0·001**
Gap-cut – reference	0·077	0·435	0·177	0·983
N-coord	0·000	0·000	−1·321	0·209
E-coord	0·000	0·000	1·383	0·190

Discussion

Studying the conflicts linked to ecological restoration is important for efficient conservation of biodiversity and for providing a basis for balanced solutions. Conflicts between different ecological goals when managing natural resources have been extensively studied in systems such as organic agriculture practices**,** which not only increase biodiversity but also benefit pest insects (Garratt, Wright & Leather 2011). The present study provides new important insights into the potential conflict between biodiversity conservation and pest control in forest systems, based on a comparison between two different, commonly used restoration measures – gap-cutting and prescribed burning. Our results show that species richness responds similarly to gap-cutting and prescribed burning, whereas the abundance of primary bark beetles and tree mortality were five times higher in burned stands. These results provide a basis for developing potential solutions to this conflict.

BARK BEETLE DIVERSITY

Forest restoration increased the general bark beetle abundance and species richness. This is not surprising as many previous studies have shown that biodiversity generally increases after various forest restoration measures (e.g. Angelstam 1998; Kuuluvainen 2002; Lindenmayer, Franklin & Fischer 2006; Toivanen & Kotiaho 2007) and that

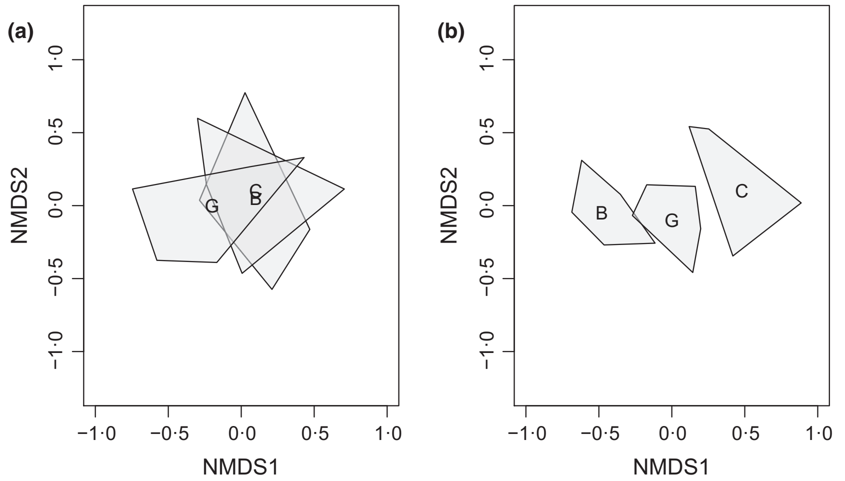

Fig. 6. Recorded bark beetle species composition in burned (B) and gap-cut (G) compared to the untreated reference stands (C), pre-restoration (a) and post-restoration (b), visualized by non-metric multidimensional scaling.

this increase includes bark beetles (e.g. Hanula *et al.* 2002; Werner 2002; Johansson *et al.* 2006; Toivanen & Kotiaho 2007; Campbell, Hanula & Outcalt 2008). The general bark beetle species richness was similar between the burned and the gap-cut areas, even though the mean volume of restoration-created dead wood was twice as high in the burned stands (Hägglund *et al.* 2015). Conversely, some studies have found a lower diversity of bark beetles in burned areas than in harvested areas (Hanula *et al.* 2002; Werner 2002), but see Toivanen & Kotiaho (2007) and Campbell, Hanula & Outcalt (2008). This difference in results can possibly be explained by low-fire intensity in our burned areas, resulting in many weak susceptible trees but relatively low direct tree mortality. Severely burned trees are inferior as breeding material for many bark beetles compared to moderately burned trees (Hanula *et al.* 2002; Johansson *et al.* 2006; Toivanen, Liikanen & Kotiaho 2009). In fact, the impact of burning on species richness may be somewhat underestimated, as indicated by the species accumulation curves that seemingly level out earlier for gap-cut and reference stands than for the burned stands (Fig. 2). This can partly be explained by the reduction in primary bark beetles from 2011 to 2012 (Fig. 3c), resulting in a relaxation of intraspecific competition. In addition, the variation in fire intensity within and among stands may increase species richness. Another reason for the observed increasing species richness (and secondary bark beetles) in reference stands may be the shorter trapping period in 2011 (see Materials and methods).

Both restoration treatments differed significantly from reference stands in assemblage composition, with burned stands being clearly more dissimilar from reference stands than gap-cut stands. Six species contributed significantly to the difference in assemblage composition between burned and reference stands, all of them were more abundant in burned stands. This difference is not surprising, as restoration treatment can generate desirable conditions for some species, but not for others. This has also been shown, for example, for trees (Keane *et al.* 2017), red-listed beetles (Hägglund *et al.* 2015) and birds (Twedt *et al.* 2010). The two most abundant bark beetles found in the burned stands – *Pi. chalcographus* and *Po. poligraphus* – are known to respond positively to the presence of fire-stressed spruces (Ehnström, Långström & Hellqvist 1995). In previous studies, *Pi. chalcographus* have been more abundant in burned areas than in harvested areas (Wikars 2002; Johansson *et al.* 2006; Toivanen, Liikanen & Kotiaho 2009). The reason for this may be that this species can utilize the thin-barked tops of trees that are not damaged, and smaller trees that are more stressed by the fire than larger trees. *Polygraphus poligraphus* can also utilize fire-killed Scots pine (Ehnström & Axelsson 2002) which may also have increased the density.

It should be noted that our results relating to bark beetle abundance and diversity may have been affected by an increase in temperature in the more open burned and gap-cut stands, which may increase flight activity in insects (Henderson & Southwood 2016). However, as we did not monitor temperatures in the different stand types, we cannot evaluate the potential influence of this.

PRIMARY BARK BEETLES

Primary bark beetle species responded more strongly than bark beetles in general to the restoration treatments. The stronger impact of burning on the abundance of primary bark beetles may be a result of the fire damaging but not killing trees, presumably making them more susceptible with lower defence and higher nutritional phloem quality (Parker, Clancy & Mathiasen 2006; Powell & Raffa 2011). The bark of trees desiccates rapidly after burning, which makes them less suitable for bark beetles (Wikars 2002; Johansson *et al.* 2006). This may explain why the majority (>80%) of primary bark beetles were found in the first trapping period (2011) after the treatment, and it indicates that the primary bark beetles respond quickly to restoration treatments, but may suffer from host tree depletion the second year and thus respond by dispersing. It could also partly be explained by the ~4 °C warmer summer temperatures in 2011 compared to 2012 (SMHI – Swedish Meteorological and Hydrological Institute) which may have increased flight activity.

The spatial distribution of the sites affected the primary bark beetle catches. This was probably because northern and mainland areas of Sweden are colder than southern/coastal areas, thus affecting bark beetle activity. This effect was marginal in comparison to the restoration treatment effect.

TREE MORTALITY AND BARK BEETLE COLONIZATION

Dead wood retention that increases the density of bark beetles and causes uncontrolled tree mortality can be devastating for valuable old forests in nature reserves, for example (Kärvemo, Rogell & Schroeder 2014). This study shows that the number of trees colonized by bark beetles after restoration treatments was highest in burned stands, whereas no difference was found between gap-cut and reference stands. A similar outcome was found for the abundance of primary bark beetles**,** indicating that this group of beetles could have been involved in killing these trees (Fig. 4). This is also supported by a relatively strong correlation between the abundance of primary bark beetles and the number of dead trees (Fig. 5) and the fact that the correlation became weaker when we included all bark beetle species. This is not necessarily evidence for a causal link, as there is a possibility that the trees might have died anyway from the restoration measures (e.g. bole char, sun exposure, etc.) and were thus not directly killed by the bark beetles.

The most abundant bark beetle species in the burned areas were *Po. poligraphus* and *Pi. chalcographus*. In a recent outbreak in north-western Sweden in 2009–2012, *Po. poligraphus* was important (88% of the trees) in colonization and possibly killing healthy spruce trees together with *I. typographus* (Schroeder 2012). *Pityogenes chalcographus* may also reach outbreak levels and can kill hundreds of young spruce stands if the tree vitality is reduced (Eidmann 1992).

In contrast to this study, previous studies have shown that bark beetle-induced tree mortality in burned areas is usually low and similar to dead wood creation (Eriksson, Lilja & Roininen 2006; Campbell, Hanula & Outcalt 2008; Komonen & Kouki 2008; Toivanen, Liikanen & Kotiaho 2009). However, these surveys were intended to study tree mortality in the unburned neighbouring forests, whereas in this study we investigated beetle densities and tree mortality within the restoration areas containing the fire damaged trees. In this study, the results reveal that prescribed burning does indeed increase the density of primary bark beetles and the number of susceptible host trees, which may increase the risk of large-scale outbreaks (Raffa *et al.* 2008).

Conclusions

To identify solutions to potential conflicts in biodiversity-oriented restoration, scientific comparisons between alternative methods are crucial. Forest restoration, based on approaches such as prescribed burning and gap cutting, are increasing world-wide and are frequently used in the boreal forests of North America and Europe; continents where outbreaks of tree-killing bark beetles are also relatively common. Bark beetle diversity was positively affected by both restoration measures studied here (burning and gap-cutting). However, burning also led to the highest number of primary beetles and a higher post-restoration tree mortality than gap-cutting, possibly at least partly due to attacks by primary bark beetles. Thus, the choice of restoration method, gap-cutting or prescribed burning, should be based on the landowners' tolerance to pest species abundance and tree mortality, as well as the positive impact on the species abundance, richness and quality. Thus, unless effects other than species richness are desired, our data suggest that gap-cutting should be the chosen method to avoid unwanted increased tree mortality at the stand level.

Authors' contributions

S.K. and J.H. conceived the ideas and designed the methodology; S.K. and T.J. collected the data; S.K. analysed the data; S.K., J.H., C.B., T.J. and J.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

All data analysed for this study, including tree mortality and bark beetle abundance and species richness, are available from Dryad Digital Repository https://doi.org/10.5061/dryad.tf1fm (Kärvemo *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Recorded abundances of bark beetle species.