Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests

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ABSTRACT

Aim Restoration of habitats may be used as a conservation tool when ecosystems have lost their natural structure, dynamics or functioning over large areas. Controlled and planned use of fire could be an effective way to restore habitats of many threatened species in boreal forests where fire suppression has been effective. We asked whether the large-scale landscape context affects the occurrence of rare and threatened species in forest habitats that have been burned to restore their fire-related structures.

Location Boreal forests in southern Finland.

Methods We designed a large-scale field experiment that included nine Pinus sylvestris forests (5–10 ha each) in southern Finland. Sites were located in two regions: (1) in eastern region with shorter management history and (2) in western region where intensive forestry has continued longer. We evaluated whether restoration of dead/burned wood is beneficial for rare and conservation-dependent species and measured the recovery of pyrophilous and red-listed insects (beetles and flatbugs) in burned forests, using standardized sampling effort. Altogether, 956 individuals of 29 red-listed and pyrophilous species were sampled.

Results Rare species colonized areas quickly, but there was a clear difference in species richness between the regions. The eastern forests harboured higher species richness after restoration. In these sites, the average species richness was 13.7 species per site, whereas in western forests it was 5.0 species per site. Similar pattern was also observed in subgroups: the corresponding numbers for pyrophilous species were 9.7 vs. 3.8, for red-listed 8.7 vs. 2.3 and for red-listed pyrophiles 4.7 vs. 1.2.

Main conclusions Introducing fire back to boreal forests can aid in the recovery of rare species, but the landscape context considerably affects the success of restoring species. If restored habitats are located in landscapes that have lost their natural properties long ago, the success of restoration seems to be more challenging than in landscapes where habitats have been modified more recently.

Keywords Fennoscandia, fire, protected forest, red-listed species, restoration ecology, Scots pine.
for the Kirtland Warbler is a classic and famous example, see e.g. Long, 2009) but very little is known about the landscape effects related to restoration success. In general terms, it is widely documented that the amount and spatial configuration of habitat at the landscape level plays a key role in the persistence of species (Fahrig, 2003; Lindenmayer et al., 2006). Thus, it is expected that also the success of restoration may depend on the landscape context.

Natural forests and their associated biota are disappearing at high rates in many parts of the world (Aksenov et al., 2002; Lee et al., 2006; Stritholt et al., 2006; Richardson et al., 2007), thus making adequate conservation areas harder to establish. In addition to deforestation, also in the regions where forest area remains – such as in North America and Europe – the structural characteristics of forests are often changing rapidly (Bryant et al., 1997; Östlund et al., 1997; Kouki et al., 2001; Richardson et al., 2007). Forests are increasingly managed for timber production. Ecological changes include the loss of structural elements – such as old trees (Andersson & Östlund, 2004) and decaying wood (Siitonen, 2001) – but also the disappearance of the disturbances that are typical in natural forests (Kouki et al., 2001; Bergeron et al., 2002; Kuuluvainen, 2002). Natural forest disturbances can be used to guide the development of biodiversity-oriented silvicultural practices in managed forests (Attiwill, 1994; Kouki, 1994; Bengtsson et al., 2000), but in protected areas more intensive restoration actions may be necessary to achieve conservation goals. Indeed, restoration of the lost natural properties and disturbances is rapidly emerging conservation tool in intensively managed forest ecosystems (e.g. Penttilä, 2004; Hyvärinen et al., 2005, 2006b; Toivanen & Kotiaho, 2007b; Vanha-Majamaa et al., 2007; Junninen et al., 2008).

Fire is regarded as the main disturbance factor in natural boreal forests both in Eurasia and North America (e.g. Zackrisson, 1977; Van Wagner, 1978; Bergeron et al., 2002). Natural landscape dynamics and patterns are rarely found in boreal regions nowadays (Richardson et al., 2007). In different parts of the boreal zone, fires may have either increased because of human activities (Yaroshenko et al., 2001; Achard et al., 2006) or decreased if fire suppression is efficient (Zackrisson, 1977; Niklasson & Granström, 2000). In Fennoscandia, effective fire suppression has almost completely eliminated fires since the late 1800s (Zackrisson, 1977; Pitkänen & Huttunen, 1999).

Several studies where forest stands have been burned have recently shown that controlled reintroduction of fire in forests has profound effects on species assemblages (Wikars & Schimmel, 2001; Saint-Germain et al., 2004; Hyvärinen et al., 2005, 2006b; Martikainen et al., 2006; Johansson et al., 2007; Toivanen & Kotiaho, 2007a,b; Vanha-Majamaa et al., 2007). However, the studies conducted so far have addressed the issue primarily on single stands and within restricted regions. It is not clear if controlled fires are equally effective for conservation purposes in different regions. For example, depending on the length of fire suppression period (that typically varies from decades to centuries), regions may currently sustain different species pools that provide colonizers to restored habitats.

In this study, we ask whether the ecological effects – as measured by the recovery of rare invertebrate species – of controlled and restorative burning of pine forests depend on the landscape context. In the study design, we use the opportunity that the recent history of the forest management has created in southern Finland: in the east, intensive management began later (1950s onwards), while in the west production and other types of intensive forest use have prevailed several centuries (Lihtonen, 1949; Kalliola, 1966; Tasanen, 2004). Furthermore, in the Russian Karelia adjacent to the Finnish–Russian border, forests have maintained their natural structures up to recent years and also forest fires are relatively common in that region (Uuttera et al., 1996; Uotila et al., 2002; Burnett et al., 2003). Consequently, species associated with fire, dead wood and other natural forest characteristics still seem to maintain diverse assemblages in eastern Finland close to the Russian border (e.g. Hyvärinen et al., 2006b; Hottola & Siitonen, 2008).

**MATERIAL AND METHODS**

**Study area**

The study region belongs to the boreal zone (Fig. 1). Intensive forest management has advanced from south and west to north and east during the past decades and centuries. Already during 1600s and 1700s, forests in west were heavily exploited, mainly for tar production. The current clear-cutting-based forestry began about 50–100 years ago and expanded quickly. Nowadays and starting from 1940 to 1960, practically all forests in southern Finland have been managed to produce timber and pulpwood. This main difference in the onset of intensive forestry is used in current study: the forests in the east are presumably closer to their natural state or still provide quite large species pools as compared with western areas. This observation is substantiated also by several studies (e.g. Hyvärinen et al., 2006b; Hottola & Siitonen, 2008). Protected areas in southern Finland cover only 5.1% of forest land and they are often established in sites that have been previously managed either by earlier selective cuttings in late 1800s and early 1900s or by (early) clear-cuttings in 1940s and 1950s (Anon, 2000). Effective fire suppression during the 1900s has practically eliminated fires from both managed and protected forests (Pitkänen & Huttunen, 1999; Anon 2008) and led to a depauperate fauna (Rassi et al., 2001; Hyvärinen et al., 2006a,b).

**Selection of the forest stands and the experimental treatments**

The study sites were located in nine currently protected forest sites in southern Finland (Fig. 1). At each site, a single stand was chosen as an experimental restoration (fire) site. All study sites had been intensively managed before they were...
established as protected areas. The forests had been clear-cut about 50 years ago and then seeded or planted. Their size was 5–10 ha. Before fire, the stands were structurally as similar as was possible (Table 1). Before the fire treatments, all of the areas lacked structural elements – such as coarse woody debris or fire-scars on the trees – that are known to be necessary habitat or breeding substrate for many threatened and rare invertebrate species (Tikkanen et al., 2006), in particular for saproxylics and pyrophiles that are covered in this study. All sites were burned in 2005 or 2006.

Sampling, identification and classification of the invertebrates

To sample invertebrates, we used 20 window traps at each site (see Hyvärinen et al., 2006a). The traps were set-up immediately – usually within a day – after the fire and the sampling period lasted for 2 months. Window traps are an efficient method to sample forest-dwelling invertebrates and, in particular, beetles (Hyvärinen et al., 2006a).

Pyrophilous or threatened saproxylic species were identified to species level. Pyrophilous and fire-favoured species tend to rapidly colonize burned areas if only they occur within the dispersal distances of species (e.g. Muona & Rutanen, 1994; Schutz et al., 1999; Wikars & Schimmel, 2001).

In total, about 200 beetle and flatbug species and 2121 individuals were identified to species level. Pyrophilous species were classified based on literature sources (e.g. the database used in Tikkanen et al., 2006) and our own experience (Hyvärinen et al., 2006b, 2009). The classification of red-listed species follows the IUCN-based red-list assessment in Finland (Rassi et al., 2001). We included species in the threat categories critically endangered (CR), endangered (EN), vulnerable (VU) and near-threatened (NT), collectively called red-listed species. We also checked from national invertebrate databases and collections (unpublished data were screened by author EH) that the geographic ranges of species overlap our study sites and that the species, thus, can potentially occur in these sites. This eliminates the possibility that large-scale environmental effects – such as climate – can have a major effect on our results. Finally, we did not sample the sites before burning treatments because our previous studies and field experience have shown that rare saproxylic and pyrophilous species are absent from intensively managed forests that lack dead wood and fire-scarred trees (e.g. Similä et al., 2002; Hyvärinen et al., 2005, 2006b).

Numerical analyses

We compared the number of species in four groups of species separately: all species (i.e. all pyrophilous and red-listed species), pyrophilous species, red-listed species (including red-listed saproxylics and red-listed pyrophilous species), and red-listed pyrophilous species. The dependent variable was the number of species observed at each site. Note that the different species groups share some of their species and, thus, they are not completely independent measures of the treatment effect.

As it is impossible to know the exact source of the colonizers, there is not an easy and justifiable way to quantitatively measure the isolation of the treated forests from the assumed source areas that are presumably in eastern Finland and Russian Karelia. Consequently, we divided the sites into two groups a priori: (1) eastern areas close to the border and with more recent onset of forestry and (2) sites in the western part of the country where intensive forestry has longer history (Table 1, Fig. 1). We found this procedure justified because the main objective was to reveal large-scale differences in the outcome of habitat restoration rather than to build predictive models on quantitative effects of landscape metrics or isolation on the occurrence of different species.

We did not post-standardize sample sizes (no. of individuals per site) prior to the analyses because the sampling effort (in terms of no. of traps and sampling period) was equal in different sites and also because standardization would not have allowed to test species-level data (identities of species would have been lost in the standardization procedure).
RESULTS
Altogether, we observed 956 individuals of 29 pyrophilous or red-listed species. Of these, 17 species were pyrophilous and 21 red-listed included nine species.

The effect of burning on species assemblages differed in the east and west (Fig. 2), indicating that region and landscape context had an effect on the outcome of restoration. If all species are included in the analysis, each of the eastern areas contained almost 10 red-listed and/or pyrophilous species more than the western areas. A similar pattern was found also among the pyrophilous species, red-listed species and pyrophilous red-listed if analysed separately (Fig. 2). Among the red-listed pyrophilous species, the eastern areas included on average over three more species than the western sites after the restoration treatment.

DISCUSSION
Our results show that when natural processes and properties of protected areas are restored, the ecological consequences may differ remarkably depending on the region where restoration is performed. To our knowledge, this is the first time that spatial context-dependency of restoration has been shown in boreal forests based on large-scale experimental evidence. Previous empirical and experimental studies (Saint-Germain et al., 2004, 2008; Hyvärinen et al., 2005, 2006b; Johansson et al., 2007; Toivanen & Kotiaho, 2007a) have shown that restorative use of fire can have a major positive influence on pyrophilous and threatened species, but these studies have been able to address the issue only on a single locality or region. The current results bear implications for successful conservation of species and for planning the management of protected areas.

One of the main questions in current conservation biology is how regional and landscape-level properties can be taken into account when designing and restoring protected areas (Paltto et al., 2006; Lindenmayer et al., 2008). Protected areas are often small and isolated from each other which is likely to increase the probability that species go locally extinct even if the habitat properties remain unchanged (e.g. Berglund & Jonsson, 2005). Successful conservation requires that also spatial landscape effects are taken into account when conservation areas are established. As shown in this study, also the success of restoration of specific habitat characteristics or stand attributes may depend on regional context. This urges for large-scale planning when designing restoration activities.

It is quite likely that the relevant scale of planning varies between different ecological and taxonomic groups, most likely because there are inherent differences in the dispersal ability of species (Paltto et al., 2006; Hedénäs & Ericson, 2008). Good dispersers, such as pyrophilous insects (Evans, 1966; Wikars, 1994; Schutz et al., 1999), are likely to tolerate habitat isolation and fragmentation better if they can compensate local extinctions with dispersal. However, many red-listed species and species of conservation concern are rare which may limit their potential for producing enough dispersing individuals (Hedénäs & Ericson, 2008), and very little is known about the taxon-specific spatial scale where species conservation should be planned and implemented.

Unfortunately, it is almost impossible to show exactly where the colonizers to the restored sites originate. In this study, we speculate that a major source area is the eastern part of the country or in Russia. The reasoning is based on the historical patterns in forest management, assuming that the more recent is the initiation of modern forestry the higher is the currently remaining species pool. This is substantiated by several studies that have documented such a pattern in our study region or in adjacent Russia (e.g. Siitonen & Martikainen, 1994; Kouki & Väänänen, 2000; Berglund & Jonsson, 2005; Hyvärinen et al., 2006b; Hottola & Siitonen, 2008; Laaksonen et al., 2008). Our assumption on the major source area is, however, not critical in relation to the main findings. There may, in fact, be small remnant populations also in western parts of the country.

Table 1 Tree and stand characteristics of the experimental forests before fire. All tree characteristics are for the Scots pine. Measurements are based on a standard relascope-based sampling within a stand except the height of the blackened (charred) bark that is based on 10 sample trees in each site.

| Site           | Size (ha) | Basal area (m²/ha) | Height (m) | Tree diameter at breast height (cm) | Height of blackened bark (m) |
|----------------|-----------|--------------------|------------|------------------------------------|-----------------------------|
| Eastern sites  |           |                    |            |                                    |                             |
| Ruunaa         | 8.2       | 25.0               | 18.0       | 19.0                               | 3.0 ± 1.4                   |
| Kakonsalo      | 5.3       | 24.5               | 14.4       | 16.0                               | 3.7 ± 1.1                   |
| Pihlajavesi    | 5.6       | 29.9               | 17.0       | 20.7                               | 3.3 ± 2.9                   |
| Mean ± SD      | 6.4 ± 1.59| 26.5 ± 2.98        | 16.5 ± 1.86| 18.6 ± 2.38                       | 3.3 ± 0.3                   |
| Western sites  |           |                    |            |                                    |                             |
| Isoajarvi      | 5.0       | 29.7               | 14.9       | 14.4                               | 4.1 ± 1.1                   |
| Kansanneva     | 9.5       | 23.0               | 16.0       | 20.0                               | 4.7 ± 1.4                   |
| Repovesi       | 9.4       | 26.8               | 15.0       | 18.4                               | 2.8 ± 1.1                   |
| Salamajari     | 4.9       | 22.0               | 10.0       | 12.0                               | 2.5 ± 1.5                   |
| Teijo          | 7.0       | 36.3               | 12.9       | 17.0                               | 1.2 ± 1.0                   |
| Puulavesi      | 6.7       | 25.0               | 17.0       | 18.0                               | 2.3 ± 1.1                   |
| Mean ± SD      | 7.1 ± 2.02| 27.1 ± 5.27        | 14.3 ± 2.51| 16.6 ± 2.93                       | 2.9 ± 0.2                   |
Based on the very long distances of the westernmost sites from the assumed major source area, it is quite likely that some species found in the most distant areas have originated from other sources (see also Saint-Germain et al., 2008). However, even if these small sources exist, this does not refute the main finding of the current study that the ecological success of restoration depends on region.

Our study focused on pyrophilous and red-listed invertebrates only. Pyrophilous species, in particular, are adapted to highly dynamic habitats of boreal forest landscape, the burned areas (Saint-Germain et al., 2008). It is thus likely that pyrophilous species are generally good dispersers and may not be representative of all the red-listed species that could benefit from fire or other restoration measures. Indeed, other taxonomic groups with high priority in conservation of biodiversity in boreal forests do not seem to respond as quickly to restoration as (pyrophilous) invertebrates do. Junninen et al. (2008) reported rather low positive influence of restoration fires on rare polypore fungi after 4 years of fire. Penttilä (2004) has shown that it may take over 10 years before polypore flora recovers and diversifies in burned areas. It is also possible that some ecological groups suffer from restoration. For example, high severity fires may cause long-term impacts on soil fauna (Malmström, 2010). Clearly, studies focusing on broader array of ecological and taxonomic groups and covering longer time spans than the current study are needed, to provide a more generally applicable basis for planning and conducting restoration activities. Notably, however, Hyvärinen et al. (2009) found that any harmful effects on beetle fauna (including also other species than saproxylics) are quite transient and the declined groups tend to return quickly to their pre-restoration state. Malmström (2010) noted that mild fires cause only short-term negative effects on soil fauna.

Finally, we would like to point out that habitats created by fires are highly transient. Typically, a single burned stand provides suitable breeding substrate for fire-adapted species for a limited time only (e.g. Saint-Germain et al., 2008). It is thus obvious that restoring a single stand is not enough to maintain species at the landscape. Rather, to safeguard spatio-temporal availability of habitat, the whole landscape and its typical fire regime must be considered when restoration measures are implemented. It is obvious that burning a single stand has no potential for facilitating long-term survival of species because it does not restore temporal and spatial continuity of fire regime at landscape-level (see also Pickett & Thompson, 1978).
CONCLUSIONS

We conclude that ecological restoration of natural forest properties, with controlled use of fire, is a highly efficient conservation measure in intensively managed boreal forest landscapes. It can rapidly transfer an intensively managed forest stand to a suitable habitat patch for several rare and threatened species. However, the short-term ecological benefit of these measures for several red-listed species depends on the region. Regional effects are most likely caused by the availability of habitat patches that can produce colonizers to restored areas. The availability of such population sources is presumably determined by the ecological history of the landscape, particularly by the duration and intensity of forest management.

Our results clearly suggest that ecologically effective habitat management and restoration activities should be planned on a broad landscape scale, taking into account the variation in potential species pools that different landscapes provide, i.e. the landscape context. The importance of landscape context has recently been emphasized also when conserving biodiversity of other ecosystems, such as agricultural areas (e.g. Tschamntke et al., 2005; Rundlöf et al., 2008). Consequently, landscape context seem to have significant role in the conservation success in very different types of habitats. However, identifying the actual landscape scale that needs to be considered may vary widely (Pickett & Thompson, 1978, Leroux et al. 2007), and its identification remains as a major challenge in regional conservation planning.

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**BIOSKETCH**

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