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SHORT COMMUNICATION

Persistence of pyrophilous insects in fire-driven boreal forests: population dynamics in burned and unburned habitats

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ABSTRACT

Several boreal insect species respond to smoke and heat generated by forest fires and use recent burns to reproduce in high numbers. Some of these species are rare or uncommon in undisturbed forests, and the contribution of recently burned habitats to their population dynamics has been deemed crucial by some to their long-term persistence. Consequently, the severe decline seen in some species in Fennoscandia has been frequently linked with fire suppression. In this paper, we explore some aspects of the spatial dynamics of pyrophilous insect populations in relation to the expected relative contribution of burned and unburned habitats to their global population dynamics. Forest fires are, throughout the boreal forest biome, generally highly aggregated in some years while rare in most other years. The low connectivity between fire events and the typical life cycle seen in these species make it improbable that recent burns act as significant population sources. This leads us to suggest that populations of pyrophilous species may be more limited by the adequacy of the unburned matrix than by the occurrence of fire events. Moreover, by combining an age-class distribution model and a dead wood availability model, we show that the quality of the unburned matrix increases in landscapes with longer fire cycles, in which pyrophilous insects should persist at higher population levels. We conclude that the degradation of the unburned habitat better explains the decline of pyrophilous insects than fire suppression alone.

Keywords

Boreal forest, forest fire, habitat connectivity, population dynamics, pyrophilous insects.

INTRODUCTION

For thousands of years, fire has been a dominating force shaping the mosaic structure of the boreal forest (Johnson, 1992; Payette, 1992; Bergeron *et al*., 2001, 2004a). This heterogeneity in the landscape produced by disturbances supports a large part of the diversity typical of this biome (Rowe & Scotter, 1973). Because of the obvious link between disturbance and diversity in the boreal forest, numerous ecologists have advocated that its management should be based on natural disturbance regimes in terms of size, shape, frequency and intensity of logging operations (Attiwill, 1994; Haila *et al*., 1994), which resulted in the widespread application of even-aged management. Concurrently, because logging and fire are often seen as 'competing' for timber resources, attempts have been made at reducing the impact of fire on allowable cuts, either through fire suppression or through post-fire salvage logging (Bergeron *et al*., 2004b). In the last few decades, the combination of such practices resulted in the general degradation of forest landscapes in terms of specific habitat elements often associated with recently disturbed sites, such as dead wood (Siitonen, 2001). Consequently, groups of organisms associated with such habitat elements appeared to decline in numbers (Wikars, 1997; Jonsell *et al*., 1998). Recently, attempts have been made at rehabilitating such species using measures targeting at creating or preserving recently burned areas, such as prescribed fires. However, at this point, our understanding of these species' population dynamics is poor, especially regarding the importance of the role played by unburned mature habitats, and it is thus debatable whether such measures alone would be enough to restore fire-associated species.

Numerous insect species dependent on dead wood that oviposit on heavily stressed or recently dead trees and that live in fire-prone ecosystems exhibit a pyrophilous behaviour (i.e. are attracted to potential substratum-rich recently burned habitats

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by smoke and/or heat). The physiology underlying such behaviour has been described in some species, particularly in Buprestidae and Cerambycidae (Coleoptera), and includes antennal receptors that detect specific smoke components and mesothoracic organs that detect infrared radiation (Evans, 1966; Schütz *et al.*, 1999; Schmitz *et al.*, 2000; Sowards *et al.*, 2001; Suckling *et al.*, 2001). In the boreal forest, where natural ecosystem dynamics are mostly driven by forest fires, pyrophily is thought to be widespread, and several studies have shown massive and immediate colonization of recent burns by insects (Gardiner, 1957; Muona & Rutanen, 1994; Dajoz, 1998; Wikars & Schimmel, 2001; Saint-Germain *et al.*, 2004a,b,c). Cerambycid genera *Acmaeops* and *Arhopalus*, and most likely *Monochamus*, and Buprestid *Oxypteris acuminata* (DeGeer), are well-known examples of pyrophilous saproxylic (i.e. insects dependent on dead wood) taxa (Wikars, 1994; Saint-Germain *et al.*, 2004c; Boulanger & Sirois, 2007). Several such species are found at very high densities in recent burns, but are uncommon or rare in unburned forests. Thus, the relative contribution of recently burned habitats to these species' population dynamics is generally expected to be high, and the decline seen in some species has been consistently linked with a lengthening of the fire cycle related to fire suppression (Anhlund & Lindhe, 1992; Wikars, 1997; Jonsell *et al.*, 1998). In this paper, we use the term 'pyrophilous' only with reference to species that have specific sensorial adaptations to detect forest fires; it thus probably excludes several secondary species that could be considered as 'fire-favoured'.

In boreal forests driven by natural disturbances, large-diameter snag recruitment mainly occurs at stand initiation, usually following large-scale fires or insect epidemics, and in mature and overmature stands, where more or less synchronous senescence occurs (Siitonen, 2001; Pedlar *et al.*, 2002). In the last few decades, north European boreal forests have been intensively managed (Esseen *et al.*, 1997; Angelstam, 1998). This management affects dead wood availability in two ways. First, fire suppression has become very efficient, and as a result less than 0.01% of Fennoscandian forests burn annually today (Granström, 2001). This represents an extension of the fire cycle from a historical average of 100 years to about 10,000 years. Second, short-rotation harvesting tends to eliminate overmature stands from the landscape. As an example, dead wood volume is reduced by 90–98% under recent management practices in Finland when comparing managed landscapes to pristine forests (Siitonen, 2001). Such a decrease in dead wood availability has led to the severe decline of numerous saproxylic species, including numerous species associated with recent burns [e.g. *Acmaeops marginatus* (F.)] (Jonsell *et al.*, 1998). The decline of pyrophilous species has been linked to efficient fire suppression, and controlled burnings are now used as a conservation tool in Fennoscandia (Wikars, 2002).

Concurrently, in North America, intensive forest management is progressing, and salvage logging (i.e. harvesting fire-killed trees in recent burns) is slowly emerging as a standard practice (Nappi *et al.*, 2004). There also, concerns about the impact of such practices on fire-associated species, most particularly pyrophilous ones, have been voiced (Nappi *et al.*, 2004; Saint-Germain *et al.*, 2004a). We should also mention that in North America, fire cycles were shown to be much shorter a mere 150 years ago across most of boreal Canada, and that further lengthening is expected at least regionally due to global warming (Flannigan *et al.*, 2001; Bergeron *et al.*, 2004b). The question whether we should expect negative impacts of the lengthening of the fire cycle on species adapted to frequent forest fires is thus highly relevant.

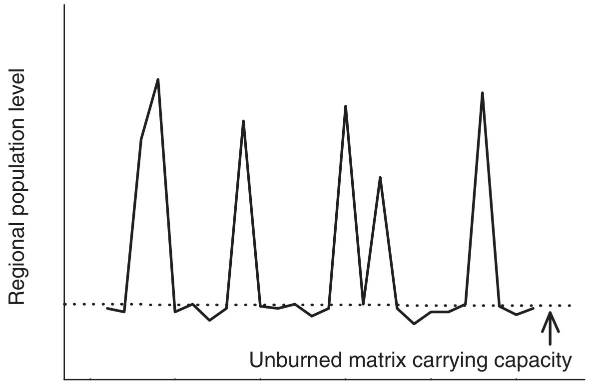
The main objective of this paper is to determine, by reviewing known aspects of the spatial dynamics of pyrophilous insect populations, whether these species could subsist being strictly fire-dependant, or if some contribution of mature unburned forests to their population dynamics would be essential to their persistence. We argue that spatial and temporal connectivity between fire events is not sufficient to maintain regional fire-induced population increases of pyrophilous species even in boreal regions where the fire cycle is short, especially when considering these insects' short-lived and discrete adult generations. We suggest that these insects breed regularly in the unburned matrix, and that it is the carrying capacity of this matrix that limits these species' populations, not recent burn availability. As a secondary objective, we used two previously published models, describing, respectively, the age-class distribution of forest stands in a landscape according to its fire cycle and dead wood availability of stands according to their age class, to determine how the carrying capacity of a given landscape varied with its disturbance regime, or whether short fire cycles are beneficial to pyrophilous species or not. We theorize that natural landscapes with short fire cycles are not necessarily beneficial to these species, as the unburned matrix carrying capacity tends to increase with fire cycle length in natural landscapes. We conclude on the conservation implications of this alternative perspective.

Habitat connectivity and population dynamics of pyrophilous insects

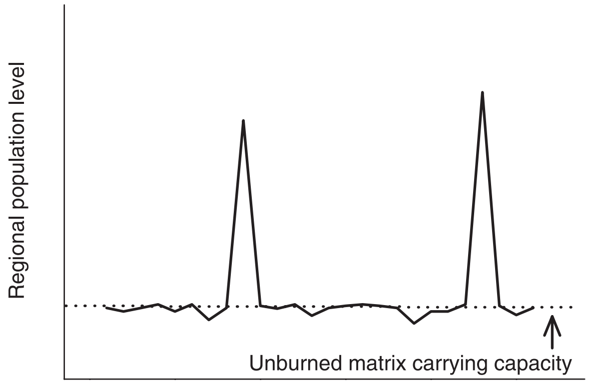
In boreal forests, severe large burns offer nearly unlimited carrying capacity for pyrophilous wood-feeders, as thousands of healthy trees die in a more or less synchronous manner. Such fire-killed trees offer egg-laying substrate for the adults and feeding substrate for the larvae. This substrate availability, coupled with the massive convergence of reproducing individuals driven by fire-produced long-range attractants, result in a significant nearly immediate increase of regional populations. However, pyrophilous wood-feeders cannot breed in the same host for multiple successive generations, all of these species being stressed-host species (*sensu* Hanks, 1999). Adults of pyrophilous Cerambycid genera such as *Acmaeops*, *Arhopalus*, and *Monochamus* can only oviposit on freshly killed trees, as early instar larvae are dependent on nutritional conditions present in the first few weeks following the death of the tree, most probably simple sugars availability (Chararas, 1981; Alya & Hain, 1985; Hanks, 1999). Fire-killed wood will be eventually colonized by dead-host species that may reproduce for multiple generations in the same substrate (Saint-Germain, 2007), but these species never show behavioural response to fire. In fact, pyrophilous behaviour would make little sense in dead-host species, as fire-created stimuli indicate recruitment of freshly killed trees, and not of more seasoned wood. Hence, the new generation must disperse and find appropriate substrate elsewhere, usually within a few weeks of emergence, which is the adult lifespan of most of these beetle species. In Fig. 1, we present a conceptual model of population response to wildfire with regard to time intervals between fires events and the carrying capacity of the unburned matrix. If a substantial proportion of the new generation is not able to find another recent burn in which they would be able to maximize their fitness, i.e. within a few weeks, the benefits derived from breeding in a recent burn in terms of regional population increase will be mostly lost, as populations will be lowered to a level determined by the carrying capacity of the unburned matrix for the following generation (see Fig. 1a). If pyrophilous species were really fire-dependant and bred exclusively in recent burns, this level would be at zero, and populations would go locally extinct, as adult generations are short-lived and discrete. Since adults cannot survive over several years, no gradual decrease in population over several generations (i.e. source-sink scenario) can be expected in such a context unless the unburned habitat is markedly unsaturated. Such non-saturation of the unburned habitat could result from highly variable yearly tree mortality rates or by suboptimal host location mechanisms, but such aspects have not been researched thus far. Some circumstances, such as variable severity fires resulting in delayed mortality and increased post-disturbance snag recruitment at edges, may prolong the population increase for a few years, but probably not at levels comparable to the one observed immediately after the disturbance.

A key question is whether habitat connectivity between recent burns is high enough in the boreal forest to consistently maintain pyrophilous insect populations at levels higher than what the unburned matrix can support. The number and intensity of fire events in the boreal forest are known to be extremely variable and unpredictable from year-to-year, being highly dependant on weather. This unpredictability of recent burn availability constitutes in our view a major problem. To illustrate this, we used a database, maintained by the SOPFEU (Société de protection des forêts contre le feu), a governmental agency mandated to prevent, detect, and suppress forest fires in the province of Quebec (eastern Canada), recording the occurrence and surface area of forest fires that took place between 1972 and 1998. On Fig. 2, we plotted (a) the number of fire events and (b) the area burned per year. These graphs show that fire events and area burned are highly aggregated in some years (perhaps hot and dry) and nearly absent in other years. Such patterns are well known and have been documented all over the northern hemisphere (Larsen, 1996; Bergeron *et al*., 2001; Kauhanen, 2002; Stocks *et al*., 2002). This suggests that populations of pyrophilous insects are likely to be brought back to lower levels on a regular basis in years with limited recently burned surface area, which occur most of the time (Fig. 2b). In such years, the quality of the unburned matrix would be the main determinant of these species' population trends.

(a) Natural landscape



(b) Fire suppression



(c) Lowered unburned matrix quality

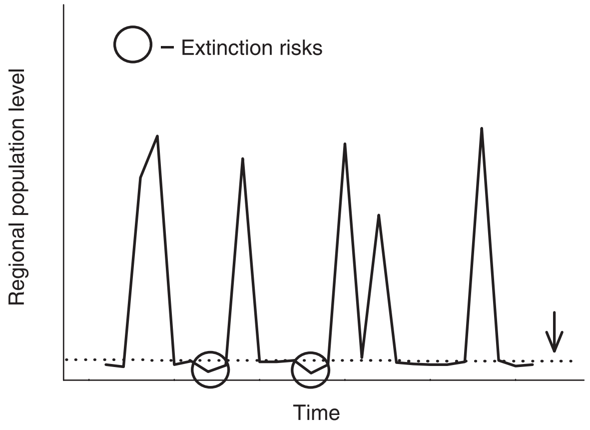


Figure 1 Theoretical population fluctuations showing oscillations around a lower level reflecting the mean carrying capacity of the unburned matrix, and population peaks following fire events, either collapsing immediately when no other fire events occur or maintaining themselves under successive fire event; (a) population dynamics in a fire-driven natural landscape; (b) dynamics in a fire-suppressed landscape, with fewer peaks associated with disturbance; (c) dynamics in a landscape with reduced matrix carrying capacity. Circles indicate extinction risks.

Another way to address the connectivity issue is to ask what the average distance between the closest fire events happening in successive years is, a distance that insects would have to travel for successive generations to breed in recent burns. To address this, we used the same database as above, but focused on a 3294-km^2 area of northern Quebec that has been investigated in terms of

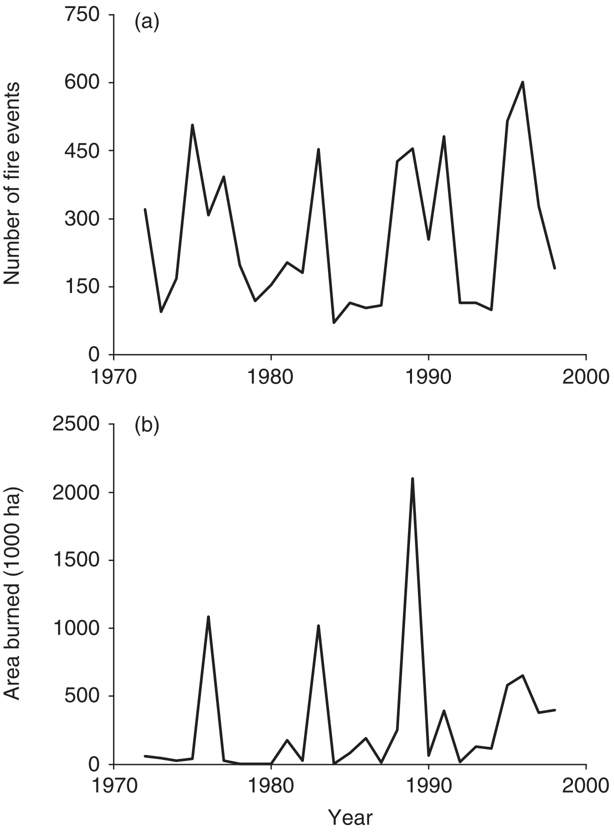


Figure 2 Number of fire events and total area burned in hectares per year between 1972 and 1998 for the province of Quebec, all causes combined.

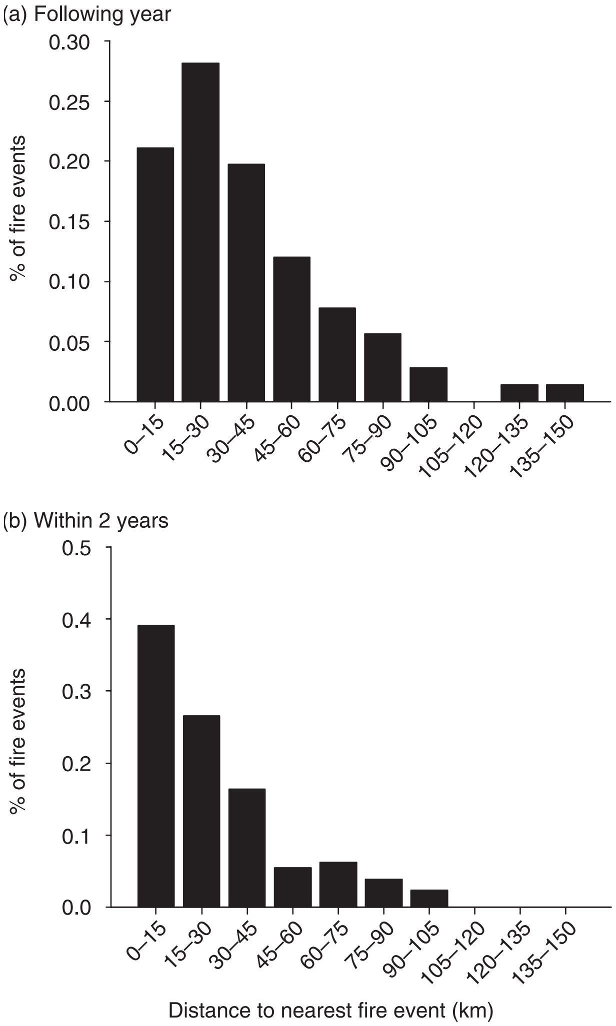


Figure 3 Distances recorded between fire events of natural causes in (a) successive years or (b) within 2 years following the initial fire, in a 3294 km^2 coniferous-dominated area in north-western Quebec, Canada, between 1972 and 1997.

fire history by Bergeron *et al.* (2001; Abitibi east, region 3). The recent regional fire cycle was estimated at 191 years, which is the shortest among the four regions of north-eastern Canada investigated by these authors. To estimate what would be recent burn connectivity in a natural landscape, we removed fires that were from documented human origin, which were not very numerous in this region. Those of which the cause was either 'undetermined' or 'unrecorded' were kept in our analysis. Using the software Arcview GIS 3.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA), we measured the distance from 144 fire events that took place between 1972 and 1997 to the closest one taking place the following year and within the following 2 years (as some insect species emerge as adults over more than 1 year following oviposition).

The average distances for 1 and 2 years were 38.5 km and 27.4 km, respectively. The distribution of the data is also shown in Fig. 3. Figure 3 shows that in about 65% of cases, the closest fire event is over 30 km away, and in 37% of cases over 60 km away. These estimates are conservative, given they assume that the fires can be detected over long distance by insects in every direction. This is not the case in reality, as the horizontal motion of the smoke plume is essentially governed by the prevailing winds, and thus mostly unidirectional (Ghoniem *et al.*, 1993). Most of these fires were probably undetectable to insects that were located upwind from the fire. Also, not all fires burned high-quality mature forests. The weather hypothesis for fire susceptibility, which states that large fires are driven by extreme weather events and occur independently of fuel load (see Agee, 1997), has gained substantial support, at least for coniferous-dominated landscapes (Bessie & Johnson, 1995; Johnson *et al.*, 1998). Under such a regime, very young stands have largely the same probability of burning as older stands. This means that in landscapes having a relatively short fire cycle, fire burns very young stands quite frequently; the proportion of recent burns being of low quality for pyrophilous saproxylic insects is thus likely to be high. As an example, thousands of hectares of ~15-year-old spruce stands burned in 1999 in central Quebec and densities of pyrophilous wood-borers were very low in these small-diameter trees (see Saint-Germain *et al.*, 2004b,c on effect of diameter on colonization).

What are the dispersal capabilities of pyrophilous insects? Unfortunately, very few estimates are available in the literature. Raske (1972) estimated that *Monochamus scutellatus* (Say)

(Coleoptera: Cerambycidae) could travel over 10 km in its adult life. This is still much less than the 30–60 km and more that insects would have to travel in a few days for successive generations to breed in recent burns. Some bark beetles can apparently disperse over distances of 40 km (Byers, 2000); to do so however, they must fly downwind. To converge towards a fire using the smoke plume as attractant would require the insect to fly upwind. Again, these observations suggest that the quality of the unburned matrix is a primary factor in these species' population dynamics, and that situations in which the contribution of recent burns is short-lived or totally absent are widespread. Supporting this statement is the detection of several beetle species exhibiting pyrophilous behaviour in recently dead trees in unburned forests, including *Acmaeops proteus* (Kirby) and *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae), when appropriate sampling methods are used (Saint-Germain, 2007). We can thus hypothesize that the habitat quality found in the unburned matrix is the real limiting factor in pyrophilous insect population dynamics, largely because of the short, discrete generations characterizing adult insects. If this is the case, do forest fires contribute in any way at maintaining higher populations of pyrophilous insects and ensuring their long-term persistence in the landscape?

The fire cycle and the carrying capacity of the unburned matrix

To demonstrate how the quality of the unburned matrix in an unmanaged landscape should vary according to the length of the fire cycle, we combined two models. First, we used a model by Van Wagner (1978) predicting what should be the age-class distribution of forest stands in a landscape according to its fire cycle. This distribution fits a negative exponential, and can be calculated from the following equation:

$$\Sigma f(x) = 1 - e^{-px} \tag{1}$$

where p equals the proportion of the whole forest that should burn every year (the reciprocal of the fire cycle) and x is the stand age in years. We generated such age-class distributions for fire cycles from 50 to 500 years at 50-year intervals (Fig. 4a). We then applied the generated age-class distributions to equations published by Hély *et al.* (2000) describing the expected snag volume (m^3 ha^{-1}) according to stand age for balsam fir (*Abies balsamea* L.):

$$y = 0.004t^2 - 0.419t + 9778 \tag{2}$$

and all species combined:

$$y = 20{,}184 \times 10^{0.004t} \tag{3}$$

where y represents snag volume and t the stand age (see Fig. 4b). Since Hély *et al.*'s equations were based on data from stands aged up to 250 years and do not reach asymptotes, we assumed that snag volume was constant in stands aged 250 years and up, to avoid unrealistic estimates of the contribution of very old stands.

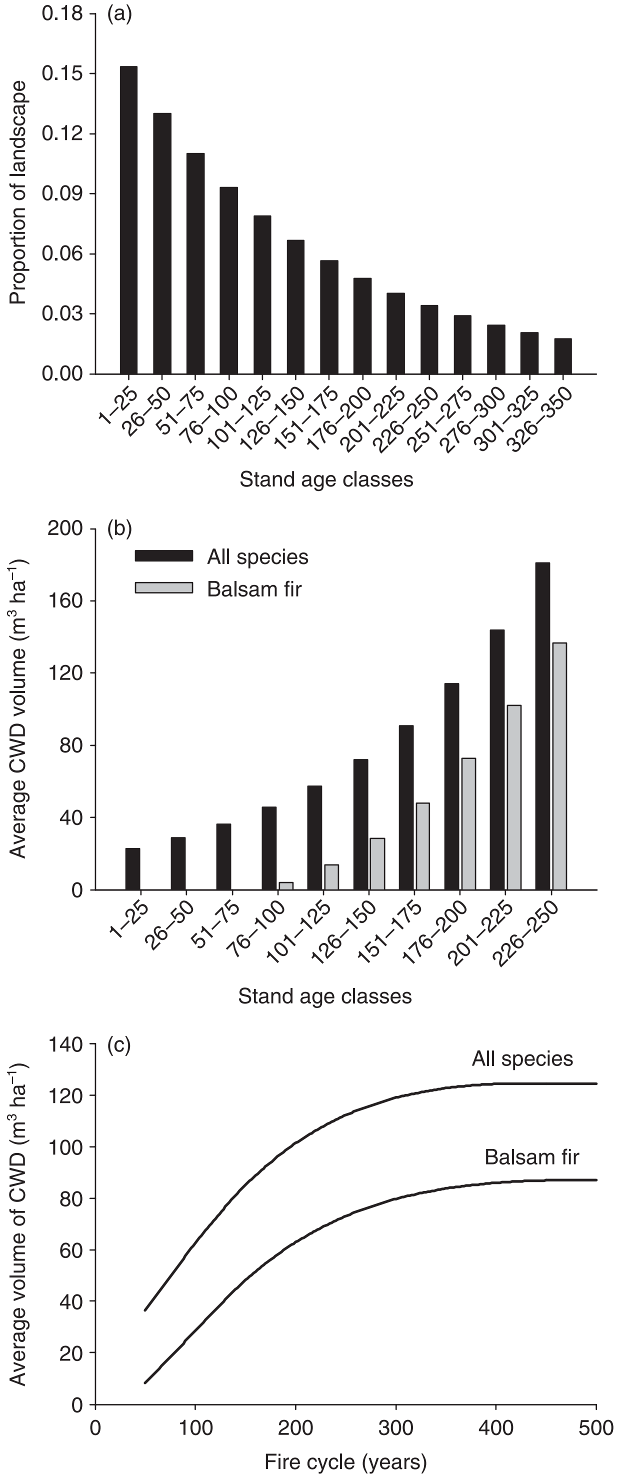


Figure 4 Average snag volume found in theoretical landscapes under a gradient of fire cycle lengths, for balsam fir and all species combined, calculated using models from Van Wagner (1978) and Hély *et al.* (2000). (a) Distribution of stand age classes in a landscape with a fire cycle of 150 years. (b) Distribution of predicted snag volume for different stand age classes. (c) Combination of the two previous models, showing average snag volume in a landscape according to its fire cycle.

The combination of the two models allowed us to produce curves describing how average snag volume should vary in a landscape according to its fire cycle, excluding the contribution of recent burns (Fig. 4c). We consider these curves to be fair estimates of the carrying capacity of the unburned matrix for pyrophilous wood-feeding species along a fire cycle gradient, despite the fact that they also incorporate decay classes not suitable for such species thriving on recently dead trees. Figure 4(c) shows that snag volume in undisturbed stands of landscapes under short to moderate fire cycles can be comparatively very low, due to low snag recruitment, as most trees do not reach senescence before being killed by fire. These results indicate that if pyrophilous insect populations are limited by the carrying capacity of the unburned matrix, these populations would be maintained at higher levels in landscapes with longer cycles or without fire altogether, as snag availability becomes much higher in such landscapes. Even if shorter fire cycles equates to higher connectivity between recent burns, the short cycle lengths needed to have sufficient connectivity to allow some level of population increase maintenance would also equate in younger landscapes with smaller trees, and thus reduced substrate availability with negative impacts on recent burn and unburned matrix carrying capacities. Even if pyrophily does not allow the maintenance of higher population levels in fire-driven ecosystems, it could have easily emerged by allowing individuals of the pyrophilous genotype to maximize their fitness when forest fires occurred, while being selectively neutral in the absence of fire.

Conservation implications

The link between the decline of pyrophilous species in Fennoscandia and intensive fire suppression may seem obvious. However, substrate availability has declined simultaneously in the managed unburned matrix, and the fact that pyrophilous species still persist in a landscape with a realized fire cycle of 10,000 years, albeit in reduced numbers, indicates that recent burns may not be a critical habitat for them. If the carrying capacity of the unburned matrix is in fact the limiting factor for these species, then the exclusion of dead wood in managed forests may be the real cause of the rarefaction of these species, by significantly lowering the carrying capacity of the unburned matrix. We believe that published cases of severe decline or extirpation of pyrophilous species (see Wikars, 1997; Jonsell *et al.*, 1998; Whitehouse, 2000) can be correlated with a degradation of unburned matrix habitat as well or better than with a lengthening in the fire cycle. If this is the case, prescribed burning alone would be of little use for the conservation of these species. Maximizing dead wood availability in the unburned matrix should also be an important goal.

Whereas fire suppression by itself may not be a significant threat to pyrophilous insects, the situation is entirely different when it comes to salvage logging. Burned stands that are logged have usually already been colonized by pyrophilous insects. Here, recent burns may become important population sinks, as the fitness of all the individuals that converged towards the fire is reduced to near zero as the standing dead wood is processed. Salvage logging is emerging as a standard practice in Canada (Nappi *et al.*, 2004) and around the world (Lindemayer *et al.*, 2004), and is actually conducted with little concern regarding the use of recent burns by wildlife.

Our analysis suggests that fire contributes little to the maintenance of wood-feeding species dependant on freshly killed snags. Paradoxically, recent burns may play a much more prominent role in the population dynamics of wood-borer species thriving on seasoned wood, which exhibit no pyrophilous behaviour at all. In the few years following the fire, snags eventually get colonized by a second wave of wood-feeders (dead-host species, *sensu* Hanks, 1999) (Saint-Germain, 2007; Saint-Germain *et al.*, in press; A. Nappi *et al.*, unpubl. data), which may occupy the same snags for several successive generations. Given the abundance of seasoned dead wood in older burns combined with the prolonged use of such sites by these species, which may span over a decade, older burns may act as source habitats for dead-host, non-pyrophilous species much more frequently than recent burns may do for pyrophilous stressed-host species using freshly killed trees. Further research will be needed to determine the exact role played by older burns in the population dynamics of dead-host wood-feeding species.

We believe that our analysis is sound at the scale of insects, which suggests that forest fires may not be a critical habitat for such species. However, for other taxa that have better dispersal capabilities and/or longer lifespan, habitat connectivity between recent burns might be high enough for them to maintain higher populations in fire-driven landscapes because of recent burn availability (see the case of the black-backed woodpecker, *Picoides arcticus*: Hutto, 1995; Hoyt & Hannon, 2002; Nappi *et al.*, 2003). Recent burns are still important and peculiar habitats of the boreal forest, and should be protected as such.

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