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Forest management and natural biocontrol of insect pests

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Current silvicultural practices are under revision as result of changing demands and pressing environmental issues. We compared the monoculture clear-cut regime commonly used during the recent decades in Europe, especially in Fennoscandia, and in North America, with three alternative forest management methods, short rotation forestry, mixed forest stands and continuous cover forestry. We evaluate how these alternative management methods are likely to affect the natural control of forest insect (regeneration pests, defoliators and bark beetles). Particular emphasis was placed on the effects of forest management on natural enemy pressure. We argue that changing forest management to any of the methods discussed will, in most cases, decrease the relative effects of bottom-up forces (resource quality and quantity) and increase the relative effects of top-down forces (natural enemy pressure) on forest pests. As population growth of the pest species presently causing most damage in European managed forests (i.e. pine weevil and spruce bark beetle) is mainly limited by bottom-up forces (quantity of suitable breeding material), changes in forest management could increase the relative importance of top-down forces by modifying stand characteristics to actively support the natural enemies. However, it remains to be investigated to what extent such alterations will result in decreased damage to trees even though some evidence points in that direction.

Keywords: population dynamics, insects, arthropods, silviculture, biological control, enemy:prey ratio

Introduction

Forests and silviculture are facing several challenges given the changing climatic conditions, use of wood and wood products and demands for consideration of environmental issues (e.g. conservation of biodiversity). In the context of climate change, forest health and adaptation of forest management are closely linked. The increased uncertainty about future growing conditions and the potential threat of invasive species add to the necessity to reconsider current management strategies.

As a response to these challenges and uncertainties, forest managers are seeking alternatives to the monoculture clear-cut forest management regime that has been dominant for the past decades in Europe, especially Fennoscandia, and North America. Adopting new forest management regimes will have economic as well as ecological effects.

Here, we focus on effects on the ecosystem service corresponding to the biological control of insect pests and, more specifically, on how natural enemies of three major insect pest types are expected to respond to changes in forest management. In many parts of northern Europe production forests are dominated by pure Norway spruce or Scots pine stands that are harvested by clear cutting. We consider this forest management method as the baseline for comparisons with three alternative silvicultural systems, namely (1) short rotation forestry without thinning, (2) stands with mixed tree species, (whereby both 1 and 2 are variations of clear-cutting regimes) and (3) continuous cover forestry with uneven-aged stands that are harvested by selective cutting (i.e. no final harvest by clear cutting). Regardless of the forest management regime used, foresters must deal with tree damage and mortality due to several types of forest insect pests (Jactel *et al.*, 2009). In Europe, the most important insect pests can be divided into three main categories; regeneration pests, defoliators and bark beetles (Björkman *et al.*, 2015). The anticipated effect of changes in the forest management strategy, and a warmer climate, on damage caused by these three pest categories are described in Björkman *et al.* (2015) and are summarized in Table 1.

Following Björkman *et al.* (2015) we consider a single representative species for each type of pest. As an example of a regeneration pest, we chose the large pine weevil (*Hylobius abietis*, hereafter referred to as pine weevil), and as a bark beetle, the Eurasian spruce bark beetle (*Ips typographus*, hereafter referred to as spruce bark beetle). For the defoliator group we assessed the effects for the entire group; however, where appropriate (i.e. mixed forests) we used two related species as examples, the common pine sawfly (*Diprion pini*) and the European pine sawfly (*Neodiprion sertifer*),

Table 1 Summary table of the expected effect of different management methods compared with the baseline clear-cut forestry on insect damage for regeneration pests (i.e. the pine weevil), defoliators and bark beetles (i.e. the Eurasian spruce bark beetle) and the putative underlying mechanisms as described in Björkman *et al*. (2015)

Method	Regeneration pests	Defoliators	Bark beetles
Continuous cover forestry			
Damage level	↓	↓	↕
Putative mechanism(s)	Reduced suitability of microclimate; reduced resource availability	More variable food plant quality;	Mainly uncertainty about storm resistance
Short rotation/no thinning			
Damage level	↑	↓	↓
Putative mechanism(s)	Increased availability of suitable reproduction sites	Reduced host plant quality;	Positive relationship between infestation and age.
Mixed forest stands[1]			
Damage level	↓	↓	↓
Putative mechanism(s)	Reduced host availability; decreased host volatile released	Reduced host plant quality (increased host defence)	Lower host availability; storm resistance unknown

[1]Björkman *et al* (2015) used as definition of mixed forest stands spruce dominated stands with birch.

which are both defoliators of Scots pine. The pine weevil is a pest of conifer seedlings planted during the first years following clear-cut. The defoliators cause damage throughout the rotation period whereas the spruce bark beetle is a threat to mature spruce forests. We selected these species because, economically, they are the most important pests during the different stages of the forestry cycle in northern Europe. Therefore, mitigating impacts from these pests should be a consideration in decisions regarding forest management strategies.

We started by performing a literature survey using ISI Web of Knowledge® (core collection) using search words for four different forest management methods (regimes; 'continuous cover', 'no thinning', 'mixed forest' and 'clear-cut') together with the search term 'forestry'. Soon it became clear that there is a publication bias of research on the baseline forestry method (clear-cut) and mixed forest stands, compared with continuous cover forestry and short rotation forestry without thinning (Figure 1). The investigation of trophic interactions in forests subject to these forestry methods appears to be lagging behind. Therefore, we conceptualize the effects of forest management on natural enemies by extrapolating from the knowledge of changes in stand structure and effects on herbivorous insects using ecological theory.

Our objectives were to evaluate and describe how changes in forest management are likely to affect damage from pests through effects on the natural enemies of these insect pests. Our findings are described using the following structure: first, the ecological theories and concepts associated with pest control in forest ecosystems are outlined. Next, we describe possible effects of the different forest management strategies on stand characteristics, followed by the potential effects of these changes in stand characteristics on herbivores and the diversity and abundance of their natural enemies. Furthermore, we discuss the expected effects on enemy pressure and how this may affect the mortality of forest pest insects. A summary of the current knowledge of the role of natural enemies in the population dynamics of the pine weevil, bark beetle and defoliators can be found in the Supplementary Material 1.

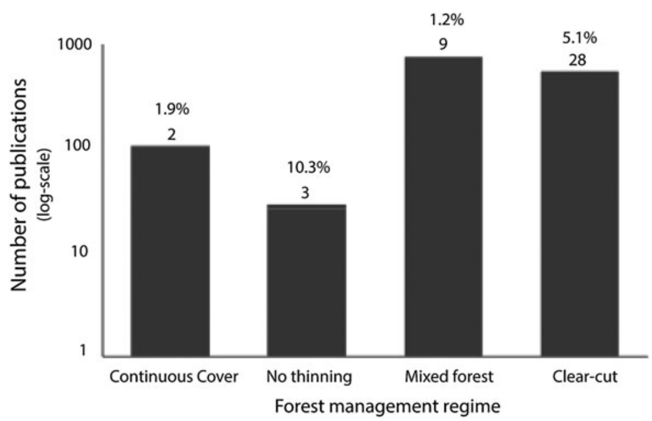

Figure 1 The number of publications found in the Web of Science (core collection) using the search terms for four different forest management methods (regimes; 'continuous cover', 'no thinning', 'mixed forest' and 'clear-cut') together with the search term 'forestry'. The figures above the bars indicate the percentage and absolute numbers of publications within the groups that also contain the word 'insect'. Search date: 13 November 2015. Note: 'no thinning' was used instead of 'short rotation' or 'short rotation' and 'no thinning' to get a good representation of papers dealing with the subject, e.g. excluding papers on forests with very short rotation periods (3 – 10 years) normally used on agricultural land.

Ecological theory and concepts related to natural biological control in forests

The basic concepts underlying the population dynamics of forest insects involve top-down (natural enemies) and bottom-up (host plant) forces acting on the reproductive success and survival of insect populations. In addition, lateral forces (competition) significantly influence the population dynamics at high population densities (Martin *et al*., 2013).

Release from enemy pressure (top-down) is considered to be a common underlying factor that drives fluctuations in many forest insect populations (Berryman, 1996). The continuity or stability of enemy pressure affects the strength and regularity of this release, and is often linked to the number of enemy species involved; few enemy species often result in low stability in enemy pressure (Macfadyen *et al*., 2009). This is a concrete example of the diversity–stability theory, which suggests that more diverse ecosystems will be more stable or more resilient to perturbations (McCann, 2000) and it has been suggested that more diverse forest systems suffer less insect damage (Jactel *et al*., 2005). A relevant hypothesis within this theory is the 'insurance hypothesis', proposing that, because different tree species and different natural enemy species are differentially susceptible to disturbance, high diversity will maintain the overall functioning of an ecosystem even when biotic and abiotic conditions are temporally disturbed (Yachi and Loreau, 1999). From the perspective of the insurance hypothesis any kind of management that increases diversity could be useful to increase the resistance of a community or ecosystem.

To describe the potential benefits of a diverse plant community Root (1973) coined the term 'associational resistance', which is now a widely accepted ecological concept encapsulating plant diversity effects on herbivores and their natural enemies (Barbosa *et al*., 2009). Associational resistance basically consists of two hypotheses, one addressing the bottom-up processes (the resource concentration hypothesis) and the other addressing the top-down processes (the natural enemy hypothesis) both of which are likely to affect the success of a herbivorous insect in a heterogeneous habitat.

The resource concentration hypothesis suggests that plants can benefit from neighbours that are not of the same species, for example, by masking of host trees for potential herbivores, because increasing tree diversity will make it more difficult for the pests to locate their resource (Riihimäki *et al*., 2005; Vehviläinen *et al*., 2007; Castagneyrol *et al*., 2013). This 'masking' can involve chemical mechanisms such as confusion of olfactory stimuli (Jactel *et al*., 2011) or physical (Dulaurent *et al*., 2012) mechanisms with other plants functioning as barriers (Barbosa *et al*., 2009).

The natural enemy hypothesis suggests that the presence of flowering plants in a diverse forest provides additional resources like nectar or pollen that are likely to attract and support more natural enemies. Further, increased levels of alternative prey in diverse forests might increase the overall levels of natural enemies and therefore the predation pressure on the pest insect (Letourneau *et al*., 2009). Positive effects of understorey enrichment are found in cases showing increased parasitoid densities and parasitism rates (Cappuccino *et al*., 1999), higher predation rates in leaf miners (Riihimäki *et al*., 2005) and leaf beetles (Stephan *et al*., 2016), and increased availability of alternate hosts leading to increased parasitism rates (Maltais *et al*., 1989).

These ecological concepts and theories describe general patterns in ecology. Many of them have been successfully used to develop 'conservation biological control' methods in agricultural systems (Barbosa, 1998) and should be taken into account when designing forest management methods to improve forest health.

Effects of forest management strategies on stand characteristics

To formulate expectations about the consequences of forest management methods, we selected the Fennoscandian clear-cut monoculture system as the baseline regime. These stands are typically dominated by Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*) which together represent more than 80 per cent of the standing volume. Thinning is conducted two to three times during the rotation period, and the rotation period is normally between 70 and 90 years, depending on the local growing conditions.

Shorter rotation forestry without thinning also concerns conifer monocultures and is expected to lead to denser forest stands, compared with the baseline regime, with a relatively high density of small-diameter stems and clear-cutting after approximately 40 years (Björkman *et al*., 2015). Continuous cover forestry represents selective cutting of individual mature trees in uneven-aged forest stands (Pommerening and Murphy, 2004). In Fennoscandia, these stands will generally be dominated by Norway spruce (Björkman *et al*., 2015). Mixed stands are defined as stands where trees of different species grow in mixtures at the same sites, i.e. 'integrated mixed stands' (Bravo-Oviedo *et al*., 2014; in contrast to 'non-integrated mixed stands', consisting of small single tree species sub plots). Thus, the alternative forest management strategies differ from the baseline in age–structure, rotation length, tree density and tree diversity (Table 2). Continuous cover forests and mixed forest stands will lead to increased habitat complexity (Gartner and Reif, 2004) mostly because of increased structural diversity (continuous forest cover) and higher compositional diversity (mixed forest stands). Understorey vegetation, i.e. the herb and shrub layer, in the stand is affected by forest management as well. In both continuous cover and mixed forest stands the understorey vegetation will be more developed as result of increased variation in canopy openness (Ares *et al*., 2010). In short rotation stands the understorey structure has less time to develop, and towards the end of the rotation more standing dead wood can be expected as a result of self-thinning in the absence of thinning operations during the rotation (Carnus *et al*., 2006).

Table 2 Overview of the differences between forest management strategies based on changes on stand characteristics

	Baseline	Continuous cover	Short rotation	Mixed stands
Tree diversity	Low	Low	Low	High
Age–structure	Even-aged	Uneven-aged	Even-aged	Even-aged
Rotation length	Long	Continuous	Short	Long
Tree density	Medium	High	High	Medium
Harvesting residuals	High	Low	High	High
Understorey	Medium	Medium	Low	High

Effects of forest management strategies on herbivores and natural enemies

The abundance of natural enemies in proportion to the available prey and the expected stability of their populations over time determine the enemy pressure on insect pests. The natural enemy pressure within a forest stand is linked to the abundance of natural enemies relative to the abundance of prey in combination with the efficiency of the natural enemies (Snyder *et al*., 2006). There are two main consequences of changes in natural enemy abundances: (1) change in the ratio between abundance of enemies and prey and (2) change in the stability of enemy abundance to maintain the prey population at non-outbreak levels. Different forest management strategies could have differential effects on the abundance and efficiency of the natural enemies, which in turn will affect the abundance and densities of the herbivore populations. Here, we describe the effects on herbivore and natural enemy from the perspective of expected changes in stand structure.

Tree diversity and age structure

Tree diversity could have positive effect on generalist herbivores as it increases resource availability; however, the opposite might be true for specialist herbivores as the resources decrease and become harder to find according to the resource concentration hypothesis (Root, 1973). The diversity of generalist natural enemies could also be higher in structurally more complex stands (Root, 1973; Jakel and Roth, 2004; Carnus *et al*., 2006), potentially increasing the pest mortality (Snyder *et al*., 2006; Letourneau *et al*., 2009). The underlying mechanism is probably the increased presence of alternative hosts in the stand that enhance the diversity of the natural enemy complex. This higher diversity is likely to stabilize the natural enemy pressure from disturbances through the 'insurance theory' (Yachi and Loreau, 1999) (Table 3A).

Understorey

Changes in understorey vegetation are not expected to directly affect the herbivores. However, understorey enrichment as a result of the use of mixtures or a change in canopy structure in continuous cover forests could increase the quantity and diversity of flowering plants in a stand. Natural enemies, such as parasitoid wasps, may extend their longevity while enhancing fecundity by using these additional nectar sources (Cappuccino *et al*., 1999; Hougardy and Grégoire, 2000; Russell 2015). The effect could be widening of the 'window-of-opportunity' to attack herbivores, increasing mortality pressure. Small mammals prefer sheltered habitats to open habitat, therefore, increased structure in the understorey could benefit the presence and activity of small mammals preying on herbivorous insects (Kollberg *et al*., 2014).

Tree density

High density of species of the same tree species could lead to decreased tree vigour as a result of increased competition for nutrients or light between the trees. The absence of thinning in short rotation stands will lead to increased presence of standing dead wood or susceptible trees as a result of self-thinning towards the end of the rotation. As the rotation is only 40 years the stand will not be suitable for the herbivores that prefer older, less vigorous trees. High tree density could benefit the movement of walking arthropod predators like ants, and many spiders might thrive in the dense vegetation and disperse more easily through the connecting canopies of individual trees (Huang *et al*., 2014). Flying enemies, on the other hand, like bats (Müller *et al*., 2013) or insect parasitoids might have difficulty navigating through the dense vegetation, but it is unclear if this could affect their efficiency. For some natural enemies, such as small mammals, tree density could decrease their abundance as a consequence of reduced understorey structure (Muzika *et al*., 2004). Increased understorey structure, after thinning or in less dense stands, increases natural enemy abundance which might increase predation rates (Hanski, 1990; Grushecky *et al*., 1998).

Rotation length

In short rotation stands, the more frequent clear-cuts will lead to increased disturbance of the habitat. This may disrupt the presence of natural enemies resulting in a time lag in re-colonization for natural enemies, releasing the regeneration pests from their enemies. For continuous cover forest the effect is opposite because the absence of large-scale clear-cuts will lead to a temporal continuity in habitat at a large scale. Continuous cover forestry will also result in a permanent presence of dying trees (caused by self-thinning) of smaller diameter as well as stumps from selective cuttings, thus providing natural enemies with alternative resources or microhabitats. During the first years after the disturbance by clear-cutting, the early successional flowering herbs and grasses are thriving and may provide food for parasitoids (Rubene *et al*., 2015) and vertebrate omnivores like small mammals that may prey on pests (Michał and Rafał, 2013).

Harvesting residuals

Tree stumps, from final cuttings and thinnings, constitute the breeding material for the pine weevil, while the other herbivore groups we consider here do not utilize this resource. Final cutting and thinning residuals in the form of stumps, tops and branches constitute breeding material for other bark beetle species and thus serve as alternative hosts for natural enemies of the spruce bark beetle (Schroeder, 1999).

Combined effects of stand characteristics on herbivore host and natural enemies

In this section, we discuss the difference in effects of the alternative forestry methods, compared with the baseline regime, on the pine weevil, defoliators and spruce bark beetle (Table 3B–D; Figure 2).

Continuous cover forestry

The main factor limiting the abundance of the pine weevil, is the availability of suitable breeding material (fresh conifer stumps; Eidmann, 1977). Under continuous cover forestry, the increased shading of stumps would increase the development time of the weevil larvae (Inward *et al*., 2012) and therefore make them more vulnerable to predation. As a result of the reduced disturbance of the understorey the diversity and number of ground

Table 3 Overview of the effects of the changes in stand characteristics on the herbivore and natural enemy in A) general and the expected effect on the pine weevil, defoliators, spruce bark beetles for B) Continuous cover forestry C) Short Rotation Forestry D) Mixed forest stands

	Tree diversity	Age structure	Understorey structure and diversity	Tree density	Rotation length	Harvesting residuals
A. Conceptual connections						
Effects on herbivores	Resource availability	Resource availability	–	Individual tree vigour through competition	Tree age–vulnerability relationship	Breeding materials
Effects on natural enemies	Alternative hosts	Complementary habitat and alternative hosts	Complementary feeding resources and habitat shelter	–	Disturbance of habitat	Alternative hosts
B. Continuous cover forestry						
	Tree diversity	Structural diversity	Understorey structure and diversity	Tree density	Rotation length	Harvesting residuals
	Low	High	Medium	High	Continuous	Low
Effect on pine weevil	–	Less resource (and more shaded breeding resources)	NA	NA	Reduced resource availability	Less breeding material
Natural enemies	Increased alternative hosts	Increased alternative hosts and habitat	Increased alternative hosts and habitat	–	Low disturbance	Alternative hosts
Effects on defoliators	–	–	–	More defence; lower palatability	–	–
Natural enemies	Increased alternative hosts	Complementary habitat	Increased additional resources;	Increased shelter for small mammals	–	–
Effects on spruce bark beetle	–	Less resource (lower density of large trees)	–	Less resource (mostly small-diameter trees)	Increased resources; always mature trees	–
Natural enemies	–	Increased alternative hosts (small-diameter trees not suitable for sbb)	Increased alternative resources	Increased alternative hosts (many small-diameter trees)	Continuity of alternative hosts (dying small trees)	Continuity of alternative hosts (many selective cuttings)
C. Short rotation forestry						
	Tree diversity	Age–structure	Understorey structure and diversity	Tree density	Rotation length	Harvesting residuals
	Low	Low	Low	High	Short	High
Effect on pine weevil	–	–	–	–	Increased breeding resources (over time)	Increased breeding resources
Natural enemies	–	–	–	–	–	–

Continued

Table 3 *Continued*

	Tree diversity	Age structure	Understorey structure and diversity	Tree density	Rotation length	Harvesting residuals
Effects on defoliators		–	–	–	–	–
Natural enemies	–	–	Few additional resources	More movement of arthropod predators between trees	High disturbance	–
Effects on spruce bark beetle	–	–	–	Less resources (smaller trees)	Less resources (shorter prop of period with large trees)	–
Natural enemies	–	–	Less additional resources for parasitoids	Increased alternative hosts and continuity (dying small-diameter trees)	–	Less alternative hosts (no thinning)
D. Mixed forest stands	Tree diversity	Age structure	Understorey structure and diversity	Tree density	Rotation length	Harvesting residuals
	High	Low	High	Medium	Long	High
Effect on pine weevil	Reduced availability of breeding resources	–	–	Reduced breeding materials	–	Reduced breeding materials
Natural enemies	Increased alternative hosts	–	–	–	–	–
Effects on defoliators	Resource availability	–	–	–		–
Natural enemies	Increased alternative hosts	More refuges for small mammals	Increased alternative resources for parasitoids	–	–	–
Effects on spruce bark beetle	Less resource	–	–	–	–	–
Natural enemies	Increased alternative hosts	–	Increased alternative resources for parasitoids	–	–	–

The content of the cells is the effect of the forest characteristics compared with the stand characteristics in the baseline. 'NA' means that that category is Not Applicable and '–' indicates no difference from the baseline.

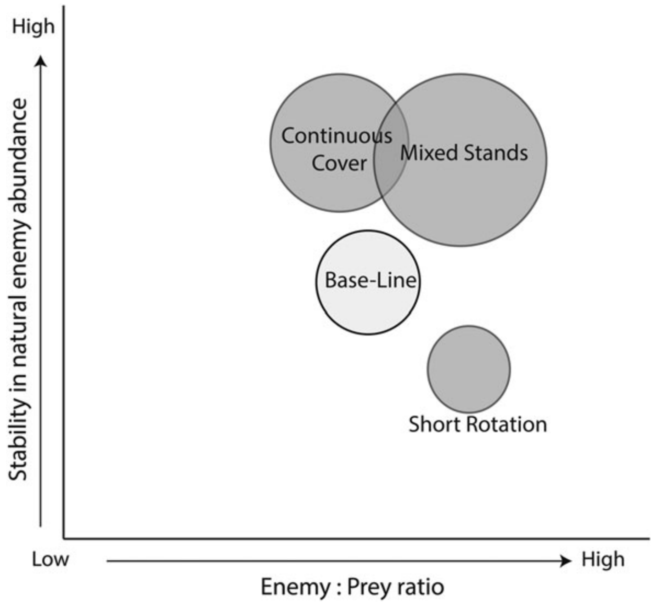

Figure 2 Visualization of the expectation for each alternative forest management regime regarding the stability of predation and the enemy: prey ratio compared with the baseline clear-cut method. The baseline is depicted in the centre of the graph, and the position of the other circles are positioned along the axis relative to the baseline. The shape illustrates the variation that can be expected with respect to the change from the baseline in the variables on the axis.

dwelling predators as well as the density of parasitoids may increase, leading to an increase in the enemy : prey ratio. However, more specialized parasitoids will most likely be able to locate their host despite the potentially lower density of suitable breeding material, and no change in efficiency of the enemies is expected.

The increased complexity of age–structure could increase the diversity of defoliators feeding in the stand. Also, increased understorey diversity will lead to enhanced longevity in parasitoids. Combined, these factors result in the expectation that the variability in natural enemy pressure over time is reduced, partly as result of a higher enemy : prey ratio.

The lower density of trees of older age classes makes the stand less vulnerable to spruce bark beetle attacks. The increased availability of substrate for alternative hosts of the natural enemies could lead to an increased enemy : prey ratio. The increased understorey and tree diversity should also benefit the natural enemies and increase their efficiency. The high continuity of alternative hosts (using small-diameter dying trees and harvesting residuals from frequent selective cuttings) should result in a more stable natural enemy pressure. An initial lower density of the bark beetle will reduce the magnitude of an outbreak after wind throw (Kärvemo *et al*., 2014).

To summarize, the availability of suitable resources is the limiting factor for the pine weevil and bark beetles in continuous cover forest stands. The defoliators will have increased number of tree age classes available. Increased diversity and stability of alternative hosts, and increased understorey structure and diversity are important to support higher numbers of natural enemies in the stands. However, it is unclear whether an increase in natural enemy efficiency can be expected (Table 3B).

Short rotation forestry without thinning

The shorter rotation will result in increased availability of breeding resources (stumps) over time for the pine weevil. As in the baseline clear-cut regime, the density of natural enemies will probably increase during the first 3 years after the final cutting, depending on the amount of recent clear-cuttings in the surrounding landscape. The enemy : prey ratio in this forest management system is expected to be similar to the baseline method and change in efficiency of the enemies is not likely.

The increased density could reduce the quality of the host plant for the defoliators and affect defoliator performance. But denser stands should encourage movement of walking arthropod enemies over the branches between the trees. Small mammals could benefit from the increased density of the canopy later in the rotation while the dense vegetation might hinder flying arthropod enemies that must navigate through a dense canopy. The enemy : prey ratio might be slightly enhanced compared with the baseline, but there is no reason to expect the efficiency of the enemies would change.

Similar to the expectation for continuous cover forestry the spruce bark beetle enemy : prey ratio should be higher compared with the baseline. Self-thinning of small-diameter trees will provide continuous substrate for alternative hosts of the natural enemies. There will be fewer large-diameter trees, suitable for the spruce bark beetle, compared with the baseline.

To summarize, short rotation forest stands provide pine weevils and defoliators with increased resources, whereas they are reduced for bark beetles. The abundance and diversity of natural enemies for the pine weevil and defoliators are not thought to change much compared with the baseline. For the bark beetle the expectation is opposite (Table 3C).

Mixed forest stands

In mixed forest clear-cuts the amount of suitable breeding material for the pine weevil will be diluted due to the presence of stumps of non-host deciduous trees. Pine weevil larvae developing in stumps of conifer species other than Norway spruce and Scots pine might exhibit reduced fitness (Thorpe and Day, 2008). Assuming that conifer species are the dominant species in the mixture, parasitoids are likely to detect their hosts and their breeding sites in this mixture of plant volatiles (deciduous and coniferous), as well as their host herbivores (but confer Zhang and Schlyter, 2004, for bark beetles).

The defoliators will have to deal with more ‘hidden’ host trees, potentially resulting in lower host location success and restricting population growth. For the natural enemies, the presence of alternative hosts could enhance their abundance. Pupal parasitism of *Diprion pini*, the common sawfly, in Bayern, Germany, was high in pure and ‘rich’ pine stands but spruce-pine mixtures (30–70 per cent) showed significantly lower parasitism rates (Herz and Heitland, 2005). For the European pine sawfly (*Neodiprion sertifer*) it was found that survival of larvae and eggs was lower in stands where pine is mixed with birch, which was mainly due to higher abundance of ants in the mixed stands (Kaitaniemi *et al*., 2007). Small mammals that prey on insects could benefit from the higher understorey diversity. Therefore, the prediction would be that mixed forest stands increase the enemy : prey ratio and also have potential to increase the predation efficiency. However, the effect of forest mixtures on natural enemies depends on the type of host herbivore and host tree (Riihimäki *et al*. 2005; Koricheva *et al*. 2006; Vehviläinen *et al*., 2008).

Using tree-species mixtures will reduce the density of the suitable host tree for the spruce bark beetle. The presence of dying trees other than spruce will provide natural enemies with a diverse range of alternative bark beetle species as prey. Research shows that the abundance of one of the spruce bark beetle's main enemies, the clerid beetle *Thanasimus formicarius*, is positively affected by the presence of pine trees (Warzee *et al*., 2006). Again the increased abundance and diversity of the understorey should support a more viable complex of natural enemies. These mechanisms should increase the enemy : prey ratio and also support a slightly higher efficiency compared with the baseline clear-cut management regime.

Thus, because of the decrease of suitable host trees, resources will decline for all three insect groups, when considering specialist defoliators. The possible increase in the presence of alternative herbivore hosts is likely to result in more diverse natural enemy communities with higher predatory efficiency (Table 3D).

Discussion

Extrapolating expectations for effects of forest management on natural enemies and their efficiency in suppressing their herbivore prey has allowed us to formulate predictions about the potential ecological consequences of changes in forest management regimes. In mixed forest stands the resource availability for the key pest species groups we considered is reduced. In addition, mixed forest stands appear to have the greatest potential to decrease the positive effect of resource availability (bottom-up) and increase negative top-down effect (increased enemy : prey ratio) on target pests. Using continuous cover stands or mixed species stands could reduce the densities of the pine weevil also at a larger scale, at the landscape level, because of the reduction of suitable breeding material (Table 1). Short rotation forestry would be effective in reducing spruce bark beetle populations through the reduction of suitable breeding material and increased natural enemy presence; however, no change is expected for defoliators, while pine weevils could even benefit from more frequent clear-cutting.

The lack of research featuring continuous cover and short rotation forestry accounts for a large part of the uncertainty in our assessment. In addition, the use of representatives for a group of insects has influenced the assessment of the different forest management methods. The pine weevil and the spruce bark beetle were chosen to represent regeneration pests and bark beetles, respectively, because they presently cause the most damage, but this does not mean that the outcomes for other regeneration pests and bark beetle species would be the same. Hence, it is not expected that one forest management method would be able to reduce the risk of damage for every insect species in the groups represented by the species discussed here. Even though our conclusions can be generalized to a certain extent, it would be necessary to assess the situation for the pests that are causing problems in other regions, prior to implementation of a management method.

The positive effects (i.e. lower damage) of associational resistance are due to (1) reduced resource concentration and plant apparency for the herbivore and (2) increased natural enemy abundance (Jactel and Brockerhoff, 2007). Associational resistance has been shown to be more effective against mono- or oligophagous pest insects (Castagneyrol *et al*., 2014). The species that currently cause the majority of damage during different phases of the rotation in managed conifer forests are more or less specialist feeders (monophagous) or have a strong preference (i.e. pine weevil) for conifers. In Northern Europe, issues with pest insects that are generalist feeders (polyphagous) are less common or severe. Even though mixed forest stands seem to be the optimal system in reducing pest insect populations, changing the forestry system from monoculture clear-cut system to mixed forest stands could exacerbate the problems with polyphagous pest insects like the nun moth (*Lymantria monacha*). This species causes severe problems in central Europe (e.g. in Poland and Hungary). There is evidence that damage by polyphagous species is higher in diverse stands, if other more palatable tree species are present, than in monocultures (Jactel and Brockerhoff, 2007), and therefore the combination of tree species in the mixture is important.

The effect of plant apparency has been shown for certain feeding guilds, depending on the tree species (Vehviläinen *et al*., 2007; Castagneyrol *et al*., 2014). Two species of specialist defoliators have also been found to respond in opposite direction to increase in tree diversity, although this observation occurred in a tropical forest (Plath *et al*., 2012). Increasing structural diversity could lead to increased numbers of refuges for herbivores, providing escape from the natural enemies as it has been shown in an agricultural context (Roubinet *et al*., 2015) and for herbivore larvae in individual host trees (Riihimäki *et al*., 2006). These caveats suggest that caution is advised when the implementation of new forestry methods is considered, as the advantages could be less obvious than one might hope.

Conclusions

The main conclusion of our assessment is that two alternative management strategies, continuous cover forest and mixed forest, compared with the prevailing clear-cutting of even-aged monoculture stands have potential to increase the enemy : prey ratio. We based our predictions on two main mechanisms that seem to be instrumental in the higher abundance and diversity of natural enemies for the groups of pest insects that were assessed: (1) the increased availability of alternative prey; (2) the provision of complementary food resources and microhabitats.

The risk of spruce bark beetle damage depends to a large extend on the vulnerability of forest stands to windthrow, the damage of the pine weevil depends on the availability of breeding substrate, and the damage of defoliators is dependent on host plant quality. The main conclusion from Björkman *et al*. (2015) is that the positive host plant effects on insect pests will be reduced by all three alternative management strategies (Table 1), with the exception of pine weevils in short rotation forestry. Combined with our conclusions on natural enemy pressure, this could mean that under alternative management regimes top-down processes might become increasingly important, compared with bottom-up effects.

In different forest insect populations it has been found that both parasitism and plant quality influence population fluctuations (Turchin, 2003; Klemola *et al*., 2010). A shift in the relative contribution of both forces could have an effect on the occurrence of population fluctuations and thus on levels of damage to forest trees. As long as this shift also means that the natural enemy pressure is more stable over time, i.e. a diverse complex of natural enemies that is not sensitive to disturbance, the result can be expected to be more stable control of pest populations in production forests. Therefore, we conclude that increasing compositional and structural diversities in the forest could reduce the risk for damage from a variety of insect pests. However, we have identified important knowledge gaps, especially with respect to the effects of continuous cover forestry and short rotation forestry that reduces the certainty of our conclusions.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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