

Forest management for invertebrate conservation

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Introduction

Insects are a diverse group of terrestrial organisms, counting at least one million of species and undoubtedly the predominant portion of animal biomass, consequently representing an essential component of every terrestrial environment. They are too often simplistically perceived as a simple nuisance or as pests due to the significant economic damages caused by a relatively small, but notable percentage of species. However, the ecological role of insects in forests is significant. Indeed, the present environment is the result of hundreds of millions of years of co-evolution between insects and plants, giving rise to the present biodiversity and complexity (Grimaldi and Engel, 2005). Due to their abundance and prevalence in forests, insects play a very important role in food webs and energy flows through different trophic levels. The variegated relationships between plants and insects vary from antagonist, such as in case of phytophagous and xylophagous species, to strictly mutualistic in case of pollinators. In turn, herbivore species are preyed by insect predators and parasitoids, which are often the best regulators of their populations. The richness of insect populations directly mirrors the diversity and abundance of vertebrates that directly feed upon them or indirectly depend on the plants/insects interactions (Price *et al.*, 2011). Finally, the rich community of detritivore and saprophagous insects contributes to the decomposition of organic matter and recycling of energy and nutrients, facilitating the colonization and the action of bacteria and fungi, thus actively participating in the complex dynamics of pedogenesis (Price *et al.*, 2011). The spatial structure and the presence of dead or decaying

wood are key components in forest environments, noticeably influencing insect diversity and their richness by supplying different microhabitats and triggering adaptations to specific niches (Campanaro *et al.*, 2011; Stokland *et al.*, 2012). Saproxylic organisms include a vast array of species depending, in at least one stage of their life cycle, on dead or decaying wood, or upon other organism living on this type of substrate (Speight, 1989); not surprisingly most of them are represented by insects and other arthropods. Many saproxylic insects are xylophagous, therefore directly degrading deadwood by feeding on it; this category includes many species with wood boring larvae, mainly belonging to Coleoptera but also members of other orders such as Hymenoptera Symphyta, Diptera and some Lepidoptera. These groups can be divided in primary and secondary saproxylics, according to the sequence on which they colonize the substrate: the first ones live on recently dead wood, while the seconds settle in more advanced stages of wood degradation (Campanaro *et al.*, 2011; Stokland *et al.*, 2012). A diverse community of predators and parasitoids both at the adult and larval stages attacks xylophagous species, while mycophagous species feed on the fungi growing on the wood. Finally, in the last stages of degradation, when wood loses its structure, it is colonized by a community not dissimilar from that of leaf litter, mainly composed of detritivores and fungivores (Campanaro *et al.*, 2011; Stokland *et al.*, 2012). The important role of insects in these environments, their diverse habitat requirements, ecological niches and notably their rapid responses to environmental changes, allow to consider some insect groups as excellent bioindicators of management and consequently of state of preservation of forests. Indeed, the strict relationship between saproxylic insects and the amount and type of dead wood implies a very strong sensitivity to forest management practices. Optimal management options to preserve this taxon in managed forests are discussed in the following paragraphs and summarised in Table 1.

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Landscape structure and insect diversity

At the landscape scale, insects populations interact, supplying and receiving colonists, and may suffer local extinctions (Price *et al.*, 2011). The colonization of new habitats is particularly important for saproxylic species since their fundamental substrate, deadwood, decays and progressively vanishes (Jonsson, 2012). The appreciation of the transient nature of the key microhabitats of these organisms is fundamental to understand how their preservation in a forest landscape cannot be ensured considering only habitat amount, but should include temporal and spatial availability (Jonsson and Ranius, 2009). For bark beetles for example, depending on scattered and ephemeral resources, a habitat patch maybe suitable for just one generation

(Lieutier *et al.*, 2004). These organisms have evolved high dispersal abilities, and the individuals can travel several kilometres of unfavourable habitat to reach new breeding sites (Bouget *et al.*, 2015). Saproxylic beetles present a very diverse range of dispersal abilities, with sex-dependent variations related to colonization behaviours (Bouget *et al.*, 2015). The importance of forest continuity for species' persistence is probably correlated with the prevailing disturbance regime, with forest types characterized with stand-scale disturbance hosting species with more efficient dispersal compared with forest dominated by gap-phase disturbance (Jonsson, 2012). Forest patches isolation affects the exchange of individuals between populations (Do and Joo, 2013), and suitable habitats could be unoccupied because of isolation from neighbouring populations. Patch size affects the richness of forest species (Ouin *et al.*, 2006): in many cases an increase of species diversity with forest patch size has been observed, and a decrease below a certain threshold. For carabid beetles for example, it is known, that they favour forest patches bigger than 1 ha (Malmyszko and Sklodowski, 2011). For less mobile species groups, like Collembola, lower threshold should be sufficient (Heiniger *et al.*, 2014). The metapopulation approach could guide landscape management with predictive models, in order to reduce extinction rates and increase colonization rates, through habitat restoration and creating stepping-stones to increase patch connectivity (Thomas and Hanski, 2004).

The implementation of ecological networks requires maintenance of both spatial and temporal heterogeneity, in a complex mosaic of patches of the same seral stage (Pryke and Samways, 2015). Agrosilvopastoral systems contributed to the preservation of high levels of saproxylic diversity (Ramirez-Hernandez *et al.*, 2014). This traditional management brought an increase of landscape heterogeneity and a high availability of senescent trees, and could be restored to effectively preserve forest landscape biodiversity. The restoration of natural forest properties should be planned on an extensive landscape scale and the potential species pools. However, if the region has suffered a long and intense exploitation the success of the operations maybe more problematic (Kouki *et al.*, 2012). In fragmented landscapes, the consideration of multiple spatial scales together with short and long-term dynamics of substrate availability (Bergman *et al.*, 2012) represents the future challenge for saproxylic biodiversity conservation.

Forest management and insect biodiversity

Forest type, stand age, openness, structure, heterogeneity and humus layer influence the distribution of invertebrates. Most of these factors can be affected by forest management. Forest type strongly influences insect species composition (Bankowska, 1980; Franklin *et al.*, 2003; Buse *et al.*, 2013). Thus, the comparison of different forest types, such as mountainous *versus* lowland, deciduous *versus* coniferous, temperate *versus* Mediterranean and pioneer *versus* old growth forests, highlights important differences in species composition. In particular, host specific herbivores and wood boring insects and their specialist natural enemies, such as parasitoids, are confined to certain forest types. Oak forests are known to have the largest diversity of insects. Many insect species included in the Habitats Directive (92/43/EEC) like *Lucanus cervus* and *Cerambyx cerdo* are specialists on oak trees. Beech forests harbour a lower insect diversity, but still host species included in the Habitats Directive (*e.g.*, *Rosalia alpina* and *Morimus funereus*). The smallest diversity maybe found in coniferous forests. Although every forest type is characterized by its own species composition, the tree diversity strongly influences communities. Indeed higher tree diversity equals insect abundance and variety (Sobek *et al.*, 2009a; Sobek *et al.*, 2009b; Sobek *et al.*, 2009c).

Forest age is an important driver of species composition. Assemblages of open habitat species change into old forest species assemblages in a gradient from clear cut to old forests. Woodland species tend to be more abundant between 30 and 60 years after cutting, suggesting a correlation with the canopy closing (Koivula *et al.*, 2002; Niemela *et al.*, 2007). In a Norway spruce stand it was found that the age category of 70 to 75 years gave the highest number of forest species of multiple taxa, while in later stages the number decreased again (Purchart *et al.*, 2013). The influence of the age stand on forest insect assemblages depends on forest type, however one of the main determining factors is the closing of the canopy.

Forest gaps increase landscape diversity and have great effects on invertebrate diversity. Gaps are mainly used by pioneer species. Forest species facultative use gaps for food resources or group there for reproduction (Chiari *et al.*, 2013). Hoverflies frequent gaps mainly to feed on nectar (Gittings *et al.*, 2006), while some beetles use stumps in gaps for reproduction (Hardersen *et al.*, 2012). The question what gap size would be most beneficial

Table 1. Summary of optimal management recommendations to preserve invertebrate biodiversity.

Landscape structure	<ul style="list-style-type: none"> • Forest patch size influences the diversity of species. • Increase forest continuity to allow metapopulation dynamics. • Build ecological networks to guarantee spatial and temporal forest heterogeneity.
Forest management	<ul style="list-style-type: none"> • Forest parameters due to management practices, such as: type, stand age, openness, structure, heterogeneity and humus layer, influence invertebrate biodiversity. • Higher tree diversity equals insect diversity. Broadleaf forests harbour more complex communities. • Insect communities depend on stand age, tending to be more abundant a few decades after cutting, then decreasing again. • Forest gaps increase landscape diversity, influencing insect species composition and abundance. To increase biodiversity larger gaps are fundamental, while to preserve species smaller gaps are preferable. A network of forest gaps, used as stepping stones and corridors, safeguards meta-population. • Forest layers sustain insect communities, therefore, the maintenance of a complex forest structure (herbaceous, shrub and canopy) is recommended. • Humus layer affects species composition: a thicker layer harbours a greater biodiversity.
Deadwood management	<ul style="list-style-type: none"> • It is a dynamic substrate: ensure continuous availability, diversifying types and decay stages. • Compensate time-lag of deadwood natural restoration actively producing deadwood. • Preserve veteran trees that have developed microhabitats and allow their replacement.

depends on the aim of the nature conservation management. If the main goal is to increase the biodiversity in forest areas, larger gaps would help to maintain subpopulations of some pioneer species which use openings as their habitat. In this case, it is also important to maintain a network of forest gaps, which are used as stepping stones and forest roads may serve as corridors in order to preserve meta-populations (Bertoncelj and Dolman, 2013). If preservation of invertebrates is highlighted, smaller gaps are more advisable (Lange *et al.*, 2014). Forest species are often not even able to cross the edge with the clear cut site or show a strong decline in abundance just a short distance from the forest edge. In non-managed forest ecosystems, small gaps are created by fallen trees. In forest management these small gaps can be created by single tree selection system. Especially, forest specialists take advantage of these small gaps. In the United States, the single tree selection harvesting increased the number of hoverfly and bee species for young stands (<5 years), while click beetles were more species-rich in old logged stands (15-20 years) (Nol *et al.*, 2006). Also in small gaps the hoverflies increased in the gaps in conifer plantages in Western Europe (Gittings *et al.*, 2006).

Insects occur over the whole vertical range of the trees. Most of different insect groups are specialized on particular forest layers (Floren and Gogala, 2002; Floren and Schmidl, 2008; Sobek *et al.*, 2009d; Birtele and Hardersen, 2012). Carabid beetles and hoverflies species are richer in the ground level (Birtele and Hardersen, 2012; Toigo *et al.*, 2013), while Heteroptera are more abundant in the canopy (Sobek *et al.*, 2009d). In the herb layer occur many herbivores and others specialists. For example, in large fields of ramson (*Allium ursinum*) specialized hoverflies occur (Hövmeyer, 1987). Also habitat generalists are positively influenced by the herbaceous layer (Toigo *et al.*, 2013). Shrub layer is important for various herbivores (Sobek *et al.*, 2009b) and is also an indicator of forest carabid species (Taboada *et al.*, 2006). Many herbivores occur in the canopy. Among hoverflies, larvae feeding in the canopy are often associated with one species of aphid (Rotheray and Gilbert, 2011). It is therefore recommended to have a rich structure in the forest.

The humus layer contains a large diversity of soil invertebrates, which live in the humus layer for food and shelter. Most of species which are occurring in the humus, such as Collembola, are detritivores, which contribute to degrade organic materials. On the other side, many predators, such as spiders and carabid beetles, frequent the humus layer for prey. The humidity should be taken into consideration, since in humid humus layers more forest invertebrate species are present (Toivanen *et al.*, 2014). The availability of the humus layer also affects species presence: a thick layer harbours many species of carabid beetles and other species (Sroka and Finch, 2006). However, when it is removed and the soil is bare, other non-forest species proliferate (Pihlaja *et al.*, 2006). The removal of the humus layer is usually correlated with open areas. In these sites, the lack of humus attracts pioneer species such as cicindelid beetles and bees, which dig nests in the bare soil.

Deadwood management for saproxylic insects conservation

A considerable proportion of species of several insects orders, such as Coleoptera and Diptera, relies on the presence of decaying wood (Stokland *et al.*, 2012). Deadwood represents both a key trophic and microhabitat resource. Nevertheless, deadwood tends

to be insufficient in managed forests, and several factors concur to its reduced natural input (*e.g.*, whole-tree and veteran trees harvesting, shortened rotations and harvesting of veteran trees) and to its lack of preservation (*e.g.*, fuelwood harvest, destruction by machinery) (Bouget *et al.*, 2012a).

Forest management not only affects the amount of available deadwood, but also influences its quality. In particular, the comparison of natural and managed forests highlights the lack of large logs in advanced decay stage in the latter case (Siitonen *et al.*, 2000). Franklin *et al.* (2000) used the term 'structural legacies' to refer to dead trees and coarse woody debris (CWD), stressing how these elements have the potential of increasing post-harvest complexity, and can promote the survival and reestablishment of forest organisms. The dynamic nature of this substrate, which chemical and physical conditions change over time, make the continuous colonisation of new suitable habitats fundamental for the persistence of saproxylic species (Lachat *et al.*, 2013). Populations must counterweigh local extinctions happening at different spatial scales, from individual logs to forest stands, with frequent colonisations to ensure their survival in a forest landscape (Jonsson *et al.*, 2005). Forest management should therefore focus on the spatial availability of deadwood and also on its temporal continuity. For deadwood to accomplish its role of structural legacy, a complete range of typologies and decay stages should be available: sufficient diameter to host sensitive beetle species (*e.g.*, Brin *et al.* 2011 suggest more than 30 cm in oak forests), and the importance of fine woody debris (FWD, diameter <10 cm) should not be undervalued (Bouget *et al.*, 2012a). Moreover, large snags have proved to support more individuals per volume unite, and diverse and rarer assemblages compared to logs (Bouget *et al.*, 2012b) and stumps represent a valuable long-lasting microhabitats (Brin *et al.*, 2012). The minimum total volume required to preserve biodiversity in productive forests could be derived from thresholds values associated to the presence of saproxylic single species or communities. For European forests, Müller and Büttler (2010) suggest to establish a landscape scale network of stands with a variable amount of deadwood comprised between 20-30 m³/ha for boreal coniferous forests, 30-40 m³/ha for mixed-mountain forests and 30-50 m³/ha for lowland forests. Increasing the amount of available deadwood to reach these minimum thresholds would take a long time if it relies on the passive self-restoration that follows the abandonment of forest activities (Bouget *et al.*, 2014). Harmon (2001) coined the world 'morticulture' to create a parallel between woody detritus production and silviculture. Thus, morticulture, acknowledging the dynamic nature of the forest system, focuses on site-specific goals for the production of deadwood. The techniques presented by Cavalli and Mason (2003) represent cost-effective intervention to actively compensate the natural time-lag of deadwood restoration (Zapponi *et al.*, 2014).

Habitat-trees and saproxylic insects

A senescent tree might essentially have two destinies: either go through a rapid death with a consequent decay succession or develop hollow and wounds, that would represent new niches for saproxylic organisms, conserving its vitality (Müller *et al.*, 2014). The first scenario would lead, in a variable amount of time, to standing and lying deadwood, while in the second one to the 'habitat-tree' (Figure 1). The slow decay of a biologically mature tree, associated with fungus and insect colonization, increases its value for saproxylic communities (Stokland *et al.*,

2012). Since the biological maturity, *i.e.*, the start of the hardwood decay and appearance of dead branches in the canopy, occurs long after the commercial maturity (Alexander, 2008), the preservation of such trees could be based on their exclusion from the harvest applying diameter thresholds, thus the scarce high ecological value elements still present in productive forests

would never be logged (Aerts, 2013). Furthermore, considering that stem shape could influence the availability of substrate for epiphytes, and branch orientation affects the suitability for bird nesting and colonisation by lichens and invertebrates, tree form could be used by foresters to target the retained structures (Newton, 2007).



Figure 1. Senescent dead wood microhabitats (nomenclature from Stokland et al., 2012 and Read, 2000). 1, Aerial roots feeding in the hole woody detritus; 2, Bark covered by mosses; 3, Small basal cavity; 4, Wet basal cavity; 5, Bird lime; 6, Bracket fungi; 7, Broken main trunk with deep cavity; 8, Coarse decaying fallen limbs on the ground; 9, Crevices in the bark; 10, Dead branches in the canopy; 11, Dead roots; 12, Dead sun exposed trunk; 13, Decaying branches; 14, Phytotelm; 15, Detached bark with dry woody detritus; 16, Dry bark pocket with fine woody detritus; 17, Dry medium dead limbs; 18, Epiphytic plants; 19, Holes in branches; 20, Lichens living on senescent trees (*i.e.*, *Lobaria pulmonaria*); 21, Lightning strike; 22, Natural water pools; 23, Open wound surrounded with callus issue; 24, Proliferation of twigs caused by bacteria; 25, Root damage from browsing; 26, Root fungal colonization; 27, Saproxylic fungal colonization; 28, Suspended dead broken limb; 29, Canker; 30, Wet pocket with fine woody detritus; 31, Woodpecker foraging holes; 32, Woodpecker nesting hole; 33, Wound with sap run flux. *Drawing by F. Mason.*

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