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Review

Influence of global warming on forest coleopteran communities with special reference to ambrosia and bark beetles

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ABSTRACT

Forest insect pests are one of the major disturbance factors in forest ecosystems and their outbreaks are expected to be more severe under the influence of global warming. Coleopterans are dominant among forest insects and their ecological functions include general detritivores, dead wood feeders, fungivores, herbivores, live wood feeders and predators. Ambrosia and bark beetles contribute to ecological succession of forests and, therefore, ecological functions of forests can be changed in response to their outbreaks. Mountain pine beetle (MPB) outbreaks are the most dramatic example of changes in the ecological functions of forest due to the outbreak of a forest insect pest altered by global warming. Composition of coleopteran species varies with latitude. However, composition of functional groups is consistent with latitude which indicates that resources available to beetles are consistent. In coleopteran communities, ambrosia and bark beetles can become dominant due to increases of dead or stressed trees due to the warming climate. This can also induce changes in the ecological functions of coleopterans, i.e. selective force to displace trees that have lower ecological fitness due to temperature increase. Therefore, recent increases in the density ambrosia and bark beetles offer a chance to study ecological processes in forests under the influence of global warming.

Contents

Introduction

Forest insect pests are one of the major threats to forest health (Dale et al., 2001; Logan et al., 2003) and they have potential to disturb forest ecosystem functions, including acting as a carbon reservoir, keeping ecological stability, and regulating energy flow and nutrient cycling (Kurz et al., 2008). These ecological functions are essential to maintain the sustainability of natural ecosystems. Under the influence of global warming, ecological functions of forest ecosystems can be changed directly or indirectly by changes in frequency, intensity, duration, and timing of disturbance factors, such as forest pests (Dale et al., 2001).

Intensity and frequency of insect outbreaks are likely to increase under the influence of global warming because insects are poikilothermic and their development is directly dependent on the ambient temperature (Jönsson et al., 2009; Tobin et al., 2003, 2008). Global warming induces changes in forest insects, including range expansion, increase in voltinism, and changes in interactions between forest pests and their food plants (Carroll et al., 2003; Jönsson et al., 2009; Tobin et al., 2003, 2008). These changes increase the risk of outbreaks which can alter habitats and modify ecological processes, both of which result in extensive ecological and economic damage (Dukes et al., 2009).

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Coleopteran insects are ideal models to study the ecological roles of forest insects under global warming conditions because they are one of the most abundant groups of insects and they serve various ecological functions including predators, herbivores, detritivores, fungivores, and live and dead wood feeders. Among the functional groups of the beetles, ambrosia and bark beetles feeding live and dead wood are major sources of tree mortality in forests (Kurz et al., 2008; Wermelinger et al., 2008). Global warming will increase the number of stressed trees which are susceptible to ambrosia and bark beetles (Kühnholz et al., 2001; Allen et al., 2010). Therefore, outbreaks of these beetles are also expected to be prevalent under the influence of global warming. Secondary ambrosia beetle species which attack only weakened or dead trees have increasingly been observed attacking living trees in both exotic and native geographic ranges of the beetles (Kühnholz et al., 2001). This phenomenon has been reported for *Platypus koryoensis* (Murayama) (Coleoptera: Platypodidade) in Korea (Choi et al., 2008), *P. quercivorus* (Murayama) in Japan (Esaki et al., 2004; Kitajima and Goto, 2004) and *P. cylindrus* (Fabricius) in Southern Europe (Cassier et al., 1996). The cause of these beetle outbreaks is likely related to global warming (Kamata et al., 2002).

In this article, I address (1) mountain pine beetle (MPB), *Dendroctonus ponderosae* (Hopkins), outbreaks in British Columbia, Canada surveyed from 2001 to 2006 to understand the outbreak mechanisms of bark beetles under the influence of global warming and their impacts on ecological functions of the forest, (2) ecological functions of coleopterans and their potential changes under the influence of global warming, and (3) outbreaks of platypodid beetles in Korea and Japan as examples of outbreaks of latent ambrosia beetles and the potential influence of global warming on outbreaks.

Mountain pine beetle (MPB) outbreak in Canada

Outbreaks of mountain pine beetle (MPB) from 2001 to 2006 were studied in Canada in the context of global warming and to determine changes in ecological functions of the forest. MPB is native to North America and is one of the major disturbance components in mature pine forests in western North America (Safranyik et al., 1974; Taylor et al., 2006). MPB can successfully attack most western pines, including ponderosa pine, *Pinus ponderosae* Lawson and lodgepole pine, *Pinus contorta* Douglas, the most important host species of MPB (Logan and Powell, 2001). Lodgepole pine is the primary host of MPB throughout most of its range (Safranyik and Carroll, 2006). Although the distribution of the lodgepole pine ranges from northern Mexico to central British Columbia, extensive outbreaks of MPB have occurred mainly in the southern interior regions of British Columbia and in the northern Rocky Mountains in the U.S. (Safranyik and Carroll, 2006). This suggests that the distribution of MPB is not restricted by the availability of suitable host trees (Carroll et al., 2003).

For the successful adaptation of MPB to an environment, temperature and precipitation are limiting factors (Logan and Powell, 2001). Life-history traits of MPB are influenced by various environmental factors, including temperature and precipitation. To complete its univoltine life cycle, the MPB requires 305 degree-days above 5.5 °C from peak flight time of the adult to 50% egg hatching of the next generation, and 833 degree-days above 5.5 °C for its total life cycle (Reid, 1962). Minimum winter temperature and average maximum temperature are also limiting factors for the spatial distribution of MPB with respect to winter mortality and adult MPB flight. An under-bark temperature at or below −40 °C causes 100% mortality and the lower threshold for MPB flight is about 18.3 °C (Reid, 1962; Safranyik and Linton, 1998). Lower precipitation is a critical factor for outbreaks of MPB because water deficit negatively affects the resistance of lodgepole pine to MPB (Ung et al., 2001).

Based on temperature and precipitation, habitat suitability of MPB in British Columbia was evaluated using GIS (Geographic Information System) maps and climate data from 1920 to 2000. The area of suitable MPB habitats increases over time, indicating climatically unsuitable habitat to MPB outbreak has changed to be suitable due mainly to temperature increases in British Columbia (Carroll et al., 2003). Actual MPB infestations from 1998 to 2002 coincided spatially with suitable habitats estimated from GIS analysis, suggesting that recent global warming induces range expansion of MPB and it is an influential factor of recent outbreaks of MPB in British Columbia (Carroll et al., 2003).

Global warming is not the only cause of MPB outbreak. Similar to other bark beetles, MPB has a preference for larger diameter trees (Shore et al., 2000) and lodgepole pine tree resistance to MPB attack decreases after 60 years of age (Safranyik et al., 1974). Most lodgepole pine trees in British Columbia are over 60 years old, indicating that forests are vulnerable to MPB outbreaks. Forest age structures that consist mainly over 60 years old trees is one of the major factors inducing MPB outbreaks in Canada along with global warming (Taylor and Carroll, 2003).

Due to global warming and tree age structure, MPB outbreaks were observed from 2001 to 2006 and the cumulative outbreak area was 130,000 km^2 by the end of 2006. As a result of the outbreaks, mass mortality of lodgepole pine was observed (Westfall, 2006). Commercial timber losses were estimated to be more than 435 million m^3, with additional losses outside commercial forests (Kurz et al., 2008).

To estimate the carbon balance from 2000 to 2020 for the south-central region of British Columbia, the impacts of the beetle, forest fires and harvesting on forest productivity were integrated and modeled. The estimated net biome production in the south-central region of British Columbia is -15.8 ± 7.9 Mt C/yr for the period from 2000 to 2020, indicating carbon loss from forest to atmosphere (Kurz et al., 2008). According to Environment Canada, the forest was a carbon sink from 1990 to 2002 but was converted to a carbon source due to MPB outbreaks. With decreasing beetle impact, the net biome production began to recover. However, by 2020, it is estimated that the net biome production will not have returned to pre-outbreak levels (Kurz et al., 2008).

Ecological function of coleopteran in forest

The “functional groups” concept is concerned with how a resource or any other ecological component is processed by different species to provide an ecosystem service or function (Blondel, 2003). The maintenance of the proper composition of functional groups is essential to maintain ecosystem functions. Therefore, ecological function approaches have increased in recent years because of current concerns about the effects of global changes, biodiversity decline, CO$_2$ increase, global warming and various other ecosystem disturbances (including pest outbreaks) on community dynamics and ecosystem functioning (Symstad et al., 2000; Wardle et al., 2000; Blondel, 2003).

Functional groups of coleopteran families are classified into 6 categories based on Lassau et al. (2005) and Borror et al. (1989): general detritivores, dead wood feeders, fungivores, herbivores, live wood feeders and predators. These groups represent various trophic levels in communities. Thus, the composition of the groups reflects the ecological roles of the coleopteran communities. Herbivores, live wood feeders and dead wood feeders are directly associated with forest primary production. Detritivores and fungivores are connected to forest decomposition processes such as nutrient cycling. Natural enemies caused up to 50% of herbivore mortality (Cornell et al., 1998), suggesting they are an important determinant of herbivore population size and are indirectly associated with forest primary production.

These functional group assemblages reflect their habitat conditions, including complexity and degree of disturbance (Ribera et al., 2001; Tews et al., 2004; Lassau et al., 2005; Buddle et al., 2006; da Silva et al., 2008), because a given community is an assemblage related to ecological functions in an ecosystem. Considering the bottom-up effects in communities (Hunter, 2001), the composition of functional groups is an indicator of forest status. Plant species composition