INTRODUCTION / INTRODUCTION

The ecology of forest insect invasions and advances in their management[1]

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Abstract: Invasions by nonindigenous forest insects can have spectacular effects on the biodiversity, ecology, and economy of affected areas. This introduction explores several critical issues that are generally relevant to invasions by forest insects to provide an extended background for this special issue of the *Canadian Journal of Forest Research* and highlights the key findings of the papers included in the issue. The topics covered address new information about (1) the role of cargo shipments as invasion pathways for the arrival of insects such as wood borers and bark beetles, (2) biogeographical effects that can influence the ecological and economic impact of insects feeding on exotic tree species, (3) the influence of biodiversity on impacts of forest insects and on the invasibility of ecosystem, and (4) recent advances in the detection, monitoring, and management of invasive species and native pests, including DNA barcoding for identification, the use of pheromones for monitoring and mating disruption, and biological control. These findings are likely to become even more important with elevated prevalence of invasions as a result of increasing global trade and international travel. Avenues of international communication and cooperation among scientists should be encouraged to enhance the sharing of information about biological invasions and to find solutions to this alarming problem.

Résumé : Les invasions d'insectes forestiers exotiques peuvent avoir des effets spectaculaires sur la biodiversité, l'écologie et l'économie des régions affectées. Cette introduction explore plusieurs questions cruciales généralement reliées aux invasions d'insectes forestiers dans le but de replacer ce numéro spécial de la *Revue canadienne de recherche forestière* dans un contexte plus large et de mettre en valeur les principaux résultats des articles qu'il contient. Les thèmes qui sont abordés portent sur les développements récents concernant (1) le rôle du transport des marchandises en tant que mode d'invasion pour des insectes tels que les xylophages et scolytes, (2) les effets biogéographiques susceptibles d'influencer l'impact écologique et économique des insectes qui s'attaquent aux espèces d'arbres exotiques, (3) l'influence de la biodiversité sur les dégâts d'insectes forestiers et sur l'invasibilité des écosystèmes et (4) les récents progrès dans la détection, le suivi et le contrôle des espèces invasives et des ravageurs indigènes, incluant les code-barres ADN pour l'identification, l'utilisation des phéromones pour le suivi des populations et la confusion sexuelle, et la lutte biologique. Ces résultats vont probablement devenir encore plus importants étant donné la fréquence élevée des invasions attribuable à l'augmentation du commerce mondial et aux voyages internationaux. La communication et la coopération internationales entre scientifiques devraient être encouragées pour favoriser les échanges d'informations sur les invasions biologiques et pour trouver des solutions à ce problème inquiétant.

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Introduction

The consequences of increasing globalization, due to elevated trade and passenger traffic among different continents, are quickly becoming evident in virtually every part of the world. One particularly noticeable aspect is the increased movement of species beyond their native ranges. Invasions by nonindigenous (alien, exotic) species can have spectacu-

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lar effects on the biodiversity, ecology, and economy of affected areas (Atkinson and Cameron 1993; Vitousek et al. 1997; Mack et al. 2000). Some of the most dramatic invasions are those by exotic forest insects (Liebhold et al. 1995; Niemelä and Mattson 1996; Haack et al. 2002). A well-known early example is the accidental introduction in the late 1800s of the gypsy moth, *Lymantria dispar*, from Europe to North America, where it has caused frequent defoliation of oaks and other broad-leaved trees over vast areas. Despite massive efforts to eradicate or contain this species, its spread has continued through much of the northeastern United States and adjacent Canadian provinces (Liebhold et al. 1995). Today, incursions by the gypsy moth and many other insects are becoming common even in some of the most remote corners of the world such as the geographically isolated archipelago of New Zealand. For example, eggs of gypsy moth are routinely found on cars, shipping containers, and other cargo imported from northeast Asia. This has not yet resulted in its establishment in New Zealand, but the recent find of a single male gypsy moth prompted an aerial spray campaign. Several other defoliating insects have established populations in New Zealand and elsewhere during the last 10 years, including the white-spotted tussock moth, *Orgyia thyellina*, (Myers and Hosking 2002), the horse chestnut leafminer, *Cameraria ohridella*, (Gilbert et al. 2004), and the painted apple moth, *Teia anartoides*, (Suckling et al. 2005*a*). Similar observations can be made for wood borers and bark beetles in many countries (Nowak et al. 2001; Haack et al. 2002; Brockerhoff et al. 2006; Haack 2006). Cases that have received much attention because they represent a significant threat to the health of forests and urban trees include the arrival of the so-called Asian longhorned beetle, *Anoplophora glabripennis*, in the United States (Nowak et al. 2001), Canada, and several European countries; the great spruce bark beetle, *Dendroctonus micans*, in the United Kingdom (Gilbert et al. 2003); the red turpentine beetle, *Dendroctonus valens*, in China (Gao et al. 2005); and the emerald ash borer, *Agrilus planipennis*, in the United States and Canada (Haack et al. 2002).

It is obvious that we need to reduce the arrival rate and future impact of such invasive species, but this would not totally mitigate the alien species problem. In addition, we need to improve our knowledge of the mechanisms by which invasions occur as well as improve our strategies for their management (Mack et al. 2000). There is also a lack of understanding of how characteristics such as biogeography and biodiversity influence the risk of establishment and the impact of exotic as well as native pests (e.g., Levine and D'Antonio 1999; Kennedy et al. 2002; Jactel et al. 2005). These and other relevant topics were addressed at a recent conference of several working parties of the International Union of Forest Research Organizations that was held in New Zealand,[4] and several significant contributions to this conference were developed further and are now combined in this issue of the *Canadian Journal of Forest Research*. Included in this issue are original contributions on the following topics:

(1) New assessments of important pathways and establishments of forest insects
(2) Biogeographical effects on exotic species
(3) Influence of biodiversity on pest impacts and ecosystem invasibility
(4) Recent advances in the detection, monitoring, and management of invasive species and native pests, including DNA barcoding for identification, the use of pheromones for monitoring and mating disruption, and biological control

This paper highlights some of the key findings of these contributions and provides an extended background to some critical issues that are generally relevant to invasions of forest insects and other species.

Pathways for the establishment of forest insects

Many introductions of forest insects go unnoticed, but a few alien insect species have become serious pests, and such invasions are among the greatest threats to forest health worldwide (Liebhold et al. 1995; Niemelä and Mattson 1996). In fact, in many countries, most of the forest insect pest species are alien, and wood borers and bark beetles feature prominently among these. Haack (2006) and Brockerhoff et al. (2006) both used historical records of insects intercepted in cargo to characterize the major pathways by which alien wood borers and bark beetles enter the United States and New Zealand, respectively. Both studies found that there was a relationship between interception frequency and probability of establishment, indicating that any future actions that might decrease the incidence of wood-boring pests in cargo could be expected to decrease the rate of new invasions. These results have important implications because they indicate that specific regulations, such as a ban on untreated wood packing material, would have important consequences on reducing one of the most critical problems facing forest health worldwide.

Both Haack (2006) and Brockerhoff et al. (2006) noted that the way port inspection data were collected limited their ability to characterize invasion pathways. These data were collected by port inspectors who reported on insects discovered in cargo that was specifically chosen for inspection, rather than as part of a statistically planned sampling program. As such, these papers highlight the need for countries to collect more extensive, statistically based data on alien species entering their country in cargo or via other pathways (e.g., passenger baggage, etc) (see also Work et al. 2004). Knowledge of invasion pathways is critical for the development of effective strategies against biological invasions (Byers et al. 2005). Given that the alien-species problem appears to be accelerating at an alarming rate, causing extensive ecological and economic damage, collection of such data to characterize invasion pathways should be a priority in the future.

Effects of biogeography and phylogeny on invasiveness

The ecological impact of pest species is often greater in their introduced range than in their native range, and this

[4] International Union of Forest Research Organizations Conference on Forest Diversity and Resistance to Native and Exotic Pest Insects, held from 10–13 August 2004 in Hanmer Springs, New Zealand.

may be the result of several factors (Mack et al. 2000). In the case of insect herbivores, these differential impacts may result from insufficient plant defences, a lack of natural enemies, or a lack of competitors in the alien habitat (e.g., Strong et al. 1984). Similar situations can occur in the reverse case, when exotic plants are exposed to new, usually native herbivores in their new territories. The degree to which introduced plants acquire new herbivores depends upon numerous biogeographical and other factors that are often overlooked and not yet well understood. This can be illustrated through a comparison of pests of pines *(Pinus* spp.) among different regions where they are planted as exotic species. For example, the North American *Pinus radiata* D. Don is planted on a large scale in several southern hemisphere countries including Chile, Australia, and New Zealand, where it has relatively few insect pests (e.g., de Groot and Turgeon 1998; Ridley et al. 2005). By contrast, in Europe where many native pine species occur, *P. radiata* is often severely attacked by the many resident pests of pines (Cobos-Suarez and Ruiz-Urrestarazu 1990), typically more so than the European pines themselves. This difference in pest load between these two alien ranges of *P. radiata* is largely explained by the fact that there are no native pines or other Pinaceae in those southern hemisphere countries. As a result, introduced pines are nearly pest free in most southern hemisphere countries. However, northern hemisphere pests may eventually colonize pines in the southern hemisphere, and when this happens their impact can be significant, especially if they are able to colonize without their natural enemies. An example of this is the case of *Rhyacionia buoliana* invading pine plantations in Chile (Lanfranco 1994 in de Groot and Turgeon 1998).

Similar trends were observed with exotic conifers introduced to Europe and their cone and seed insects as shown by Roques et al. (2006). Introduced conifers that have congeneric European species (e.g., pines and spruces) recruited many specialist cone and seed insects, which often cause more significant damage than on their European host trees. In contrast, conifers without close relatives in the European flora (e.g., Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and the “cypress” genera *Chamaecyparis* and *Cryptomeria*) recruited few native cone and seed insects, and they generally suffer little damage. Interestingly, when such insects follow their hosts to an exotic region, they may cause more damage than in the native territory. This is the case with the Douglas-fir seed chalcid, *Megastigmus spermotrophus*, in Europe (Roques et al. 2006), again a pattern of “greater fitness” in the absence of constraints experienced in the native region (Mack et al. 2000). This suggests that exotic trees may generally experience greater damage from their associated pests when these are released from their antagonists (this is known as the “enemy release hypothesis”). More complex relationships may occur in cases involving the next trophic level; an example of this occurs when introduced tree pests recruit natural enemies from closely related native insects (see comments below on Jactel et al. (2006)).

The two key messages from these cases are (1) the floristic context in which an exotic tree species occurs is an important determinant of its susceptibility to native insects; and (2) that it may take a long time for such insects to colonize hosts in an exotic environment — in the case of *P. radiata* in New Zealand very few insects have arrived in over a century — but the eventual arrival of such insects may have particularly significant consequences. Thus, a reliance on exotic trees in forestry increases the need to exclude pest introductions.

Influence of biodiversity on pest impacts and invasibility of forests

Apart from the role of biogeographical effects and recruitment limitations considered above, the outcome of introductions depends on several other factors, including the life-history traits that predispose some introduced species to become more invasive than others (i.e., their invasiveness) (e.g., Grotkopp et al. 2002), and the susceptibility of the community to become invaded by these species (i.e., its invasibility) (Mack et al. 2000; Moore et al. 2001). There has been much debate about whether a lack of diversity makes communities more invasible. In some cases, species-rich communities are thought to be more resistant to invasion (Elton 1958; Levine and D’Antonio 1999; Hooper et al. 2005) because they leave fewer vacant niches or they are better able to exploit local resources (Knops et al. 1999; Naeem et al. 2000; Tilman 2004). However, invasibility may increase as community diversity increases when the richness of native species occurs as a result of favourable environmental conditions or biotic interactions that also benefit invaders (Moore et al. 2001; Howard et al. 2004; Von Holle 2005).

A recent meta-analysis showed that in a majority of published cases mixed forests experience fewer insect pest problems than pure forests (Jactel et al. 2005), and this could also apply to exotic pests. In some cases this can be attributed to the presence of nonhost tree species in diverse stands, which can physically reduce the apparency of host trees or disrupt the host odour recognition by insect herbivores (Huber and Borden 2001; Zhang and Schlyter 2004). However, Koricheva et al. (2006), studying boreal forest communities, did not find any effect of tree species diversity on resistance to pathogens or to insect or vertebrate herbivores. In fact, in many cases that involve polyphagous insects, mixed forests have greater levels of attack than forests with less tree species richness (Jactel et al. 2005). This was also demonstrated by Koricheva et al. (2006), who report that generalist herbivores often cause more damage in mixed boreal forests than in less rich forests. The main reason for this appears to be that in mixed forests polyphagous pests can “spill over” onto less palatable tree species, leading to associational susceptibility (White and Whitham 2000). It is noteworthy that many of the worst invasive forest pest insects are polyphagous species, including gypsy moth, fall webworm, and Asian longhorned beetle.

On the other hand, plant communities with greater species richness are thought to have a greater suite of natural enemies of insect herbivores, for example, because there are more alternative prey species (Root 1973). An example of this principle has been reported by Jactel et al. (2006) for an invasive forest insect in pine forests on the Mediterranean island of Corsica. Maritime pine (*Pinus pinaster* Ait.) in mixed forests with Corsican pine (*Pinus nigra* Arnold) was consistently less susceptible to damage from an alien scale insect, *Matsucoccus feytaudi*, than pure maritime pine stands. This was attributed to the effects of a predator, *Elatophilus nigricornis*, an insect that normally preys on *Matsucoccus pini*, the endemic scale found on *P. nigra*, which was able to shift to *M. feytaudi*. In this example it is evident that the more diverse forest community is less invasible.

Further studies are therefore needed to better clarify the relationship between forest diversity and invasibility by pest insects. Filling these knowledge gaps would provide new tools for predicting the risk of invasion and suggest new forest management options for increasing forest resistance to pest insect invasion.

Recent trends in the detection and monitoring of invasive species and native pests

Reducing the rate of arrival and the establishment of alien species are just some of many activities that are necessary for addressing the increasing problem of invasions by alien forest pest species. Even if nations adopted more stringent international quarantine and inspection programs, the sheer volume of international trade is likely to insure that some invasions will still take place in the future. To manage these invasions, numerous methods exist to detect, identify, monitor, and control pest insects during the successive stages of the invasion process between arrival, establishment, and range expansion. A significant advance in the detection and identification of insects was the recent development of DNA-based methods, commonly known as DNA "barcodes", to identify species. A major advantage of this method is the ability to identify immature stages of insects, such as eggs and larvae, as well as damaged specimens, which is often difficult with conventional identification methods. Ball and Armstrong (2006) report on their development of a DNA-barcoding method, based on the sequencing of a short fragment of the mitochondrial gene *COI*, to identify 20 species of lymantriid moths. They were able to correctly identify 100% of 93 mock unknown individuals that were tested. This method can be very useful, particularly with cryptic species and immature life stages that are otherwise not easily identified. For example, larvae of longhorned beetles (Cerambycidae) that are commonly found in imported wooden packaging materials and other wooden items may be very difficult to identify, and it could take years until conventionally identifiable adults can be reared from the material. DNA-based methods hold much promise for such cases, but a prerequisite is that DNA databases exist for all relevant taxa, which will take some time to develop. Ball and Armstrong (2006) suggest that if this relatively easy method came into general use, a global invasive and pest species gene database could be developed to provide a standardized tool for biosecurity managers around the world.

To detect and monitor nonindigenous insects, pheromones are useful because they are typically highly species specific and can attract insects from a large distance. Moth sex pheromones were successfully employed to detect, delimit, and monitor several recent arrivals to New Zealand, including the white spotted tussock moth (Myers and Hosking 2002), gypsy moth, and gum leaf skeletonizer, *Uraba lugens* (Nolidae) (Suckling et al. 2005*a*). A challenge with the use of pheromones for the monitoring of populations is the difficulty of interpreting trap catches. For example, it is not clear to what degree pheromone trap catches are representative of the local abundance and temporal distribution of a species. This question was addressed by Bentz (2006) in a study of mountain pine beetle, *Dendroctonus ponderosae*, one of the most destructive bark beetles, which currently has a massive outbreak over a large area in northwestern North America. The results indicate that pheromone trap catches of bark beetles do not closely reflect the numbers and temporal patterns of beetles emerging locally. This suggests that pheromone traps also sample individuals that have dispersed over some distance, and that influences from local, natural pheromone sources may also influence trap catch (Bentz 2006). These are important findings that need to be kept in mind when trap data are interpreted. There appears to be a lack of understanding of how insects respond to pheromone sources at different times of their life cycle, for example, immediately after emergence or later after some dispersal has taken place.

Progress in the management of invasive species and native pests

Sex pheromones can also be used for the disruption of orientation or mating, as a direct control tool. This is becoming an increasingly important component in integrated forest pest management programmes. Gillette et al. (2006) showed that an aerially applied pheromone successfully reduced infestation levels of *Eucosma sonomana* and *Rhyacionia bushnelli* (Lepidoptera: Tortricidae), species which can cause considerable damage particularly in young stands of pines in the western United States. Similar mating disruption methods were considered during an eradication campaign against the painted apple moth (Lymantriidae), which was introduced to Auckland, New Zealand, but eventually not employed because the pheromone is thermally labile (El-Sayed 2005).

Once a nonindigenous species has invaded and shows significant pest potential, one of the most effective approaches to reducing the impacts of an alien pest is classical biological control, in which natural enemies are located in the species' home range and introduced to their exotic range with the expectation that they will exert some regulatory effect, thereby minimizing pest impacts (Pschorn-Walcher 1977). An excellent example of the use of classical biological control is provided by Lamb et al. (2006), which describes work being conducted to characterize the impact of an introduced predacious beetle, *Laricobius nigrinus*, on populations of the hemlock woolly adelgid, *Adelges tsugae*, in the eastern United States. Adelgids are notoriously difficult targets for the application of classical biological control because no parasitoids are known to attack adelgids worldwide (Obricky and Kring 1998). Thus, predators are the most likely candidate for biological control of this adelgid. Interestingly, *L. nigrinus* did not originate in the adelgid's native habitat of Asia, but instead was collected from western North America, where the adelgid previously invaded but is not a serious pest. Lamb et al. (2006) present data suggesting that the predator has a substantial effect on host adelgid populations and thus holds promise that this pest species might ultimately be controlled.

Cultural methods represent another approach to mitigating the impacts of invasions by alien forest pest species. There is a rich history in the use of silviculture to minimize the impacts of native forest pest species (Waters and Stark 1980) but investigations of this approach to reduce alien pest impacts are still evolving. A central tenant in many silvicultural approaches to reducing susceptibility to invasions is that forest diversity decreases invasibility; however, this concept remains somewhat controversial (as discussed above). In the paper by Jactel et al. (2006), this theory is explored to explain variability among stands in the abundance of the exotic scale insect *M. feytaudi* in Corsica. This work provides a novel explanation of how forest diversity affects alien pest impacts and ultimately could lead to more effective silvicultural approaches to managing this and other pest species.

Concluding remarks

Stemming the growing tide of alien forest insects is undoubtedly a task of global significance. The studies in this issue highlight new findings about various stages of the invasion process ranging from pathways for wood borers and bark beetles to conditions that predispose some forest types or environments to be more invasible than others. Advances in the management of introduced and native forest pests are also presented, and these are similarly relevant for our ability to reduce the impact of invasive forest pests. Several recent eradication campaigns against the white-spotted tussock moth (Myers and Hosking 2002) and the painted apple moth (Suckling et al. 2005*b*), both in New Zealand, successfully combined various strategies including trapping for delimitation and monitoring, aerial application of *Bacillus thuringiensis*, and the mass release of sterilized males. These examples demonstrate that well-executed programmes can indeed achieve eradication of invasive insects, if they are implemented before a species is widespread. However, such programmes are extremely costly, and a reduction of the arrival rate of invasive species should be the primary goal.

Given trends of ever-increasing global trade and international travel, the problem of biological invasions is likely to intensify in every part of the world. With the magnitude of the ecological and economic impacts posed by these invasions on forest ecosystems, more work is urgently needed to mitigate these damages. A critical aspect of such research is international cooperation. Given that pest species are moving about the globe at an accelerating rate, it is essential that we increase avenues of communication and cooperation among scientists in different parts of the world. It is only by sharing and comparing information about pests of global significance that scientists might be able to find solutions to this alarming problem.

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References

Atkinson, I.A.E., and Cameron, E.K. 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. Trends Ecol. Evol. **8**: 447–451.

Ball, S.L., and Armstrong, K.F. 2006. A universal DNA-based identification system for insect pests: a test case with the Lymantriidae (Lepidoptera). Can. J. For. Res. **36**. This issue.

Bentz, B.J. 2006. Mountain pine beetle population sampling: inferences from Lindgren pheromone traps and tree emergence cages. Can. J. For. Res. **36**. This issue.

Brockerhoff, E.G., Bain, J., Kimberley, M., and Knížek, M. 2006 Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Can. J. For. Res. **36**. This issue.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E., and Hayes, D. 2002. Directing research to reduce the impacts of nonindigenous species. Conserv. Biol. **16**: 630–640.

Cobos-Suarez, J.M., and Ruiz-Urrestarazu, M.M. 1990. Problemas fitosanitarios de la especie *Pinus radiata* D. Don en España, con especial referencia al Pai's Vasco. Bol. San. Veg. Plagas, **16**: 37–53.

de Groot, P., and Turgeon, J.J. 1998. Insect-pine interactions. *In* Ecology and biogeography of *Pinus*. *Edited by* D.M. Richardson. Cambridge University Press, Cambridge, UK. pp. 354–380.

El-Sayed, A.M., Gibb, A.R., Suckling, D.M., Bunn, B., Fielder, S., Comesky, D., Manning, L.A., Foster, S.P., Morris, B.D., Ando, T., and Mori, K. 2005. Identification of sex pheromone components of the painted apple moth: a tussock moth with a thermally labile pheromone component. J. Chem. Ecol. **31**: 633–657.

Elton, C.S. 1958. The ecology of invasions by animals and plants. Methuen, London.

Forbush, E.H., and Fernald, C.H. 1896. The gypsy moth, *Porthetria dispar* (Linn.). Wright and Potter Printing Co., Boston, Mass.

Gao, B., Wen, X., Guan H., Knížek M., and Žďárek, J. 2005. Distribution and attack behaviour of the red turpentine beetle, *Dendroctonus valens,* recently introduced to China. J. For. Sci. **51**: 155–160.

Gilbert, M., Fielding, N., Evans, H.F., and Grégoire, J.C. 2003. Spatial pattern of invading *Dendroctonus micans* (Coleoptera: Scolytidae) populations in the United Kingdom. Can. J. For. Res. **33**: 712–725.

Gilbert, M., Grégoire, J.-C., Freise, J.F., and Heitland, W. 2004. Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer, *Cameraria ohridella*. J. Anim. Ecol. **73**: 459–468.

Gillette, N.E., Stein, J.D., Owen, D.R., Webster, J.N., and Mori, S.R. 2006. Mating disruption of *Eucosma sonomana* and *Rhyacionia bushnelli* (Lepidoptera: Tortricidae) using aerially applied microencapsulated pheromone. Can. J. For. Res. **36**. This issue.

Grotkopp, E., Rejmánek, M., and Rost, T.L. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. Am. Nat. **159**: 396–419.

Haack, R. 2006. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can. J. For. Res. **36**. This issue.

Haack, R.A., Jendek, E., Liu, H., Marchant, K.R., Petrice, T.R., Poland, T.M., and Ye, H. 2002. The emerald ash borer: a new exotic forest pest in North America. Newsl. Mich. Entomol. Soc. **47**(3–4): 1–5.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., and Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. **75**: 3–35.

Howard, T.G., Gurevitch, J., Hyatt, L., Carreiro, M., and Lerdau, M. 2004. Forest invasibility in communities in southeastern New York. Biol. Invasions, **6**: 393–410.

Huber, D.P.W., and Borden, J.H. 2001. Angiosperm bark volatiles disrupt response of Douglas-fir beetle, *Dendroctonus pseudotsugae*, to attractant-baited traps. J. Chem. Ecol. **27**: 217–233.

Jactel, H., Brockerhoff, E., and Duelli, P. 2005. A test of the biodiversity–stability theory: meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. *In* Forest diversity and function. Temperate and boreal systems. *Edited by* M. Scherer-Lorenzen, Ch. Körner, and E.-D. Schulze. Ecol. Stud. 176. Springer, Berlin. pp. 309–344.

Jactel, H., Menassieu, P., Vetillard, F., Gaulier, A., Samalens, J.C., and Brockerhoff, E.G. 2006. Tree species diversity enhances resistance of maritime pine forest to invasion by the bast scale, *Matsucoccus feytaudi* (Homoptera: Margarodidae). Can. J. For. Res. **36**. This issue.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D., and Reich, P. 2002. Biodiversity as a barrier to ecological invasion. Nature (London), **417**: 636–638.

Knops, J.M.H., Tilma, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E., and Groth, J. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol. Lett. **2**: 286–293.

Koricheva, J., Vehviläinen, H., Riihimäki, J., Ruohomäki, K., Kaitaniemi, P., and Ranta, H. 2006. Diversification of tree stands as a means to manage pests and diseases in boreal forests: myth or reality? Can. J. For. Res. **36**. This issue.

Lamb, A.B., Salom, S.M., Kok, L.T., and Mausel, D.L. 2006. Confined field release of *Laricobius nigrinus* (Coleoptera: Derodontidae), a predator of the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in Virginia. Can. J. For. Res. **36**. This issue.

Levine, J.M., and D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos, **87**: 15–26.

Liebhold, A.M., MacDonald, W.L., Bergdahl, D., and Mastro, V.C. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. For. Sci. Monogr. **30**: 1–49.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. **10**: 689–710.

Moore, J.L., Mouquet, N., Lawton, J.H., and Loreau, M. 2001. Coexistence, saturation and invasion resistance in simulated plant assemblages. Oikos, **94**: 303–314.

Myers, J.H., and Hosking, G. 2002. Eradication. *In* Invasive arthropods in agriculture: problems and solutions. *Edited by* G.J. Hallman and C.P. Schwalbe. Science Publishers, Enfield, N.H. pp. 293–307.

Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T., and Gale, S. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos, **91**: 97–108.

Niemelä, P., and Mattson, W.J. 1996. Invasion of North American forests by European phytophagous insects. BioScience, **46**: 741–753.

Nowak, D.J., Pasek, J.E., Sequeira, R.A., Crane, D.E., and Mastro, V.C. 2001. Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. J. Econ. Entomol. **94**: 116–122.

Obricky, J.J., and Kring, T.J. 1998. Predaceous coccinellidae in biological control. Annu. Rev. Entomol. **43**: 295–321.

Pschorn-Walcher, H. 1977. Biological control of forest insects. Annu. Rev. Entomol. **22**: 1–22.

Ridley, G.S., Dick, M.A., and Bain, J. 2005. Pests, diseases and disorders. *In* Forestry handbook. *Edited by* M. Colley. New Zealand Institute of Forestry, Christchurch, New Zealand. pp. 232–235.

Root, R.B. 1973. Organisation of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracae*). Ecol. Monogr. **43**: 94–125.

Roques, A., Auger-Rozenberg, M.-A., and Boivin, S. 2006. Does a lack of native congeners limit colonization of introduced conifers by indigenous insects in Europe? A synthesis of North American and European faunal records on Douglas-fir and some Cupressaceae. Can. J. For. Res. **36**. This issue.

Strong, D.R., Lawton, J.H., and Southwood, R. 1984. Insects on plants. Harvard University Press, Cambridge, Mass.

Suckling, D.M., Gibb, A.R., Dentener, P.R., Seldon, D.S., Clare, G.K., Jamieson, L., Baird, D., Kriticos, D.J., and El-Sayed, A.M. 2005*a*. *Uraba lugens* (Lepidoptera: Nolidae) in New Zealand: Pheromone trapping for delimitation and phenology. J. Econ. Entomol. **98**: 1187–1192.

Suckling, D.M., Charles, J., Allan, D., Chaggan, A., Barrington, A., Burnip, G.M., and El-Sayed, A.M. 2005*b*. Performance of irradiated *Teia anartoides* (Lepidoptera: Lymantriidae) in urban Auckland, New Zealand. J. Econ. Entomol. **98**: 1531–1538.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proc. Natl. Acad. Sci. USA, **101**: 10 854 – 10 861.

Vitousek, P.M., Antonio, C.M.D., Loope, L.L., Marcel, R., and Westbrooks, R. 1997. Introduced species: a significant component of human-caused global change. N.Z. J. Ecol. **21**: 1–17.

Von Holle, B. 2005. Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. J. Ecol. **93**: 16–26.

Waters, W.E., and Stark, R.W. 1980. Forest pest management: concept and reality. Annu. Rev. Entomol. **25**: 479–509.

White, J.A., and Whitham, T.G. 2000. Associational susceptibility of cottonwood to a box elder herbivore. Ecology, **81**: 1795–1803.

Work, T., McCullough, D., Cavey, J., and Komsa, R. 2005. Arrival rate of nonindigenous insect species into the United States through foreign trade. Biol. Invasions, **7**: 323–332.

Zhang, Q.H., and Schlyter, F. 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. Agric. For. Entomol. **6**: 1–19.