Anthropogenic effects on interaction outcomes: examples from insect-microbial symbioses in forest and savanna ecosystems

Diana L. Six[1], Michael Poulsen[2,3], Allison K. Hansen[4], Michael J. Wingfield[5], Jolanda Roux[6], Paul Eggleton[7], Bernard Slippers[8] and Timothy D. Paine[9]

(1) Department of Ecosystem and Conservation Sciences, College of Forestry and Conservation, The University of Montana, Missoula, MT 59812, USA.
(2) Department of Bacteriology, University of Wisconsin, Madison, WI 53706, USA.
(3) Section for Ecology and Evolution, University of Copenhagen, Copenhagen 2100, Denmark.
(4) Department of Ecology and Evolutionary Biology, West Campus, Yale University, PO Box 27388, West Haven, CT 06516–7388, USA.
(5) Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, 0002, Republic of South Africa.
(6) Department of Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria 0002, Republic of South Africa.
(7) Natural History Museum, London SW7 5BD, United Kingdom.
(8) Department of Genetics, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria 0002, Republic of South Africa.
(9) Department of Entomology, University of California, Riverside, CA 92521, USA.

Diana L. Six
Email: diana.six@cfc.umt.edu

Abstract

The influence of humans on ecosystem dynamics has been, and continues to be, profound. Anthropogenic effects are expected to amplify as human populations continue to increase. Concern over these effects has given rise to a large number of studies focusing on impacts of human activities on individual species or on biotic community structure and composition. Lacking are studies on interactions, particularly mutualisms. Because of the role of mutualisms in ecosystem stability, such studies are critically needed if we are to begin to better understand and predict the responses of ecosystems to anthropogenic change. Most organisms are involved in at least one mutualism, and many in several. Mutualisms facilitate the ability of partners to exploit particular habitats and resources, and play a large role in determining ecological boundaries. When change disrupts, enhances, or introduces new organisms into a mutualism, the outcome and stability of the original partnership(s) is altered as are effects of the symbiosis on the community and ecosystem as a whole. In this paper, using examples from six microbe-insect mutualisms in forest and savanna settings, we showcase how varied and complex the responses of mutualisms can be to an equally varied set of anthropogenic influences. We also show how alterations of mutualisms may ramify throughout affected systems. We stress that researchers must be cognizant that many observed changes in the behaviors, abundances, and distributions of organisms due to human activities are likely to be mediated by mutualists which may alter predictions and actual outcomes in significant ways.

Introduction

Humans are the most powerful biological force affecting ecosystems on Earth. In forest and savanna ecosystems, anthropogenic effects have been, and remain, considerable. Such effects are expected to increase as human populations grow and pressures on these systems concomitantly increase. As the impacts and extent of human activities intensify, it is imperative that we understand how they will influence the intricate mutualisms that so strongly influence ecosystem functions and processes.

Forest and savanna ecosystems are home to much of the biodiversity on our planet. They also provide many of the critical ecosystem services humans require for survival (Costanza 1997). However, these ecosystems are also among those most impacted by human activities. Deforestation continues at a rapid rate in many parts of the world as humans convert vast areas to agricultural and urban uses (Wade *et al*. 2003; Kowero *et al*. 2006). Forests and savannas that remain are often fragmented, reducing effective population sizes, increasing extinctions, and reducing or halting migration (Saunders *et al*. 1991; Cushman 2006; Aguilar *et al*. 2006). In many forests, human practices such as logging, removal of preferred species, selective growth of desired species, and fire suppression have led to compositional and demographic changes (e.g., conversion of old growth to younger, less diverse forests), which in turn have led to an array of emergent problems including increases in pests, changes in fire regimes, and reduced biodiversity and ecosystem resilience (Fuller *et al*. 1998; McCullough *et al*. 1998; Keane *et al*. 2002). Agricultural expansion into forests and savannas has likewise impacted the function and resiliency of these ecosystems. The human introduction (both accidental and intentional) of exotic organisms is directly modifying these ecosystems with cascading effects on native biota (Lindenmayer and Noss 2006). In addition, anthropogenic warming is directly and indirectly altering many forest and savanna ecosystems through effects on the frequency, intensity, seasonality, and extent of disturbance, and on plant survival, pathogen susceptibility, soil community composition and function, and insect population responses (Dale *et al*. 2001; Logan *et al*. 2003; Kurz *et al*. 2008). Changes in disturbance regimes and temperature and precipitation patterns due to global warming are driving ecosystem shifts that can be accompanied by drastic changes in species abundance and distributions, and numerous extinctions (IPCC 2007). Interactions of anthropogenic factors can challenge ecosystems further. For example, climate change is predicted to result in substantially altered geographic ranges for many organisms (Parmesan and Yohe 2003). However, many organisms will not be able to track areas suitable for their survival if their habitat is severely fragmented (Erasmus *et al*. 2002; Thomas *et al*. 2006).

Considerable attention has been directed towards understanding and mediating effects of anthropogenic change on forest ecosystems. This attention has primarily focused on individual organisms, particularly the very abundant (e.g., pests) or the very rare (e.g., threatened and endangered), or on community-level analyses assessing impacts on biodiversity. Studies have rarely considered impacts on interactions involving multiple trophic levels (Davis *et al*. 1998; Janson *et al*. 2009; Six 2009). In particular, very little attention has been given to effects of anthropogenic change on mutualisms, despite the fact that these symbioses are among the most important drivers of ecosystem function, structure, and process (Boucher *et al*. 1982; Margulis and Fester 1991; Douglas 1994; Maynard Smith and Szathmary 1995; Del-Claro and Torezan-Silingardi 2009; Kiers *et al*. 2010), and alterations in their composition and outcomes are likely to ramify throughout affected systems (Six 2009; Kiers *et al*. 2010).

In this paper, we consider the manner in which anthropogenic changes to forest and savanna ecosystems can directly and indirectly influence symbioses and result in feedbacks that ultimately influence the ecosystem as a whole (Fig. 1). We confine our treatment to mutualisms occurring between insects and microbes. Both groups are highly sensitive to their environment and respond rapidly to change, and together, make up a vast portion of the biodiversity of these ecosystems. Very importantly, mutualisms involving these groups include key ecosystem engineers as well as pests. Indeed, it is participation in mutualisms that have allowed these organisms to become so highly successful and influential in the ecosystems within which they occur.

In the next sections, we discuss six insect-microbial symbioses that affect forests and savannas in significant ways. Each is affected by anthropogenic change, although the type of human activity influencing each symbiosis and the response by the symbioses vary considerably. In each case, effects on these symbioses, and subsequently on the ecosystems within which they occur, are already, or likely will become, profound.

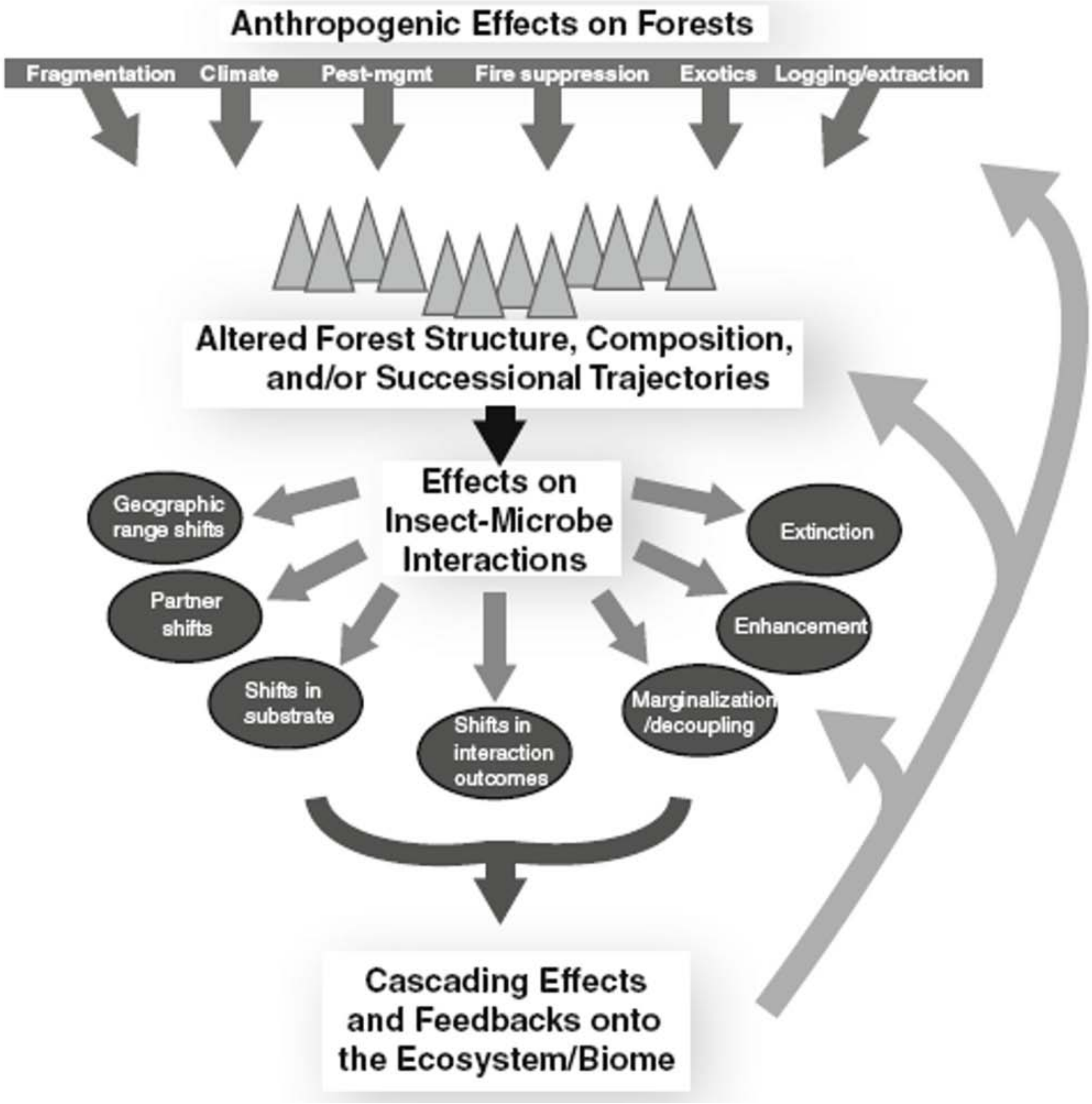

Figure 1. Anthropogenic effects on forests.

Forest/savanna insect–microbe mutualisms affected by anthropogenic forces

Bark beetle-fungus symbioses

Bark beetles (Coleoptera: Curculionidae, Scolytinae) colonizing conifers commonly form symbioses with fungi. However, the type of interaction can vary from facultative to obligate, and from mutualistic to commensal to antagonistic (Six 2003; Six and Wingfield 2011). Bark beetles construct galleries under the outer bark in the phloem layer where they lay eggs and the larvae feed. As parent beetles construct galleries they inoculate the tree with symbiotic fungi that then grow in both phloem and sapwood. In the context of beetle nutrition, phloem is a nutrient poor substrate. Bark beetles have evolved two strategies for contending with this problem. Some construct long feeding galleries and consume large amounts of phloem relative to their final adult size (Ayres *et al*. 2000). These species do not appear to gain benefit from feeding on fungi and the fungi they carry are not highly specific. Other bark beetles use fungal associates to compensate for the nutritional limitations of their diet, particularly low levels of nitrogen and a lack of usable sterols (Ayres *et al*. 2000; Bentz and Six 2006; Bleiker and Six 2008). These beetles construct short feeding galleries and spend much of their development feeding on phloem colonized by fungi or in chambers where they feed mainly on fungi (Six and Paine 1998; Ayres *et al*. 2000). These associations appear to be obligate mutualisms; without fungal feeding, beetle fecundity and size is reduced (Six and Paine 1998; Bleiker and Six 2007) and reproduction may not occur (Six and Paine 1998). Fungi involved in these associations are typically highly consistent with, and specific to, their beetle hosts (Six 2003). Indicative of their reliance on fungi, many of these beetles have evolved complex, highly selective integumental structures called mycangia, in which they carry fungi to new trees enhancing the potential for vertical transmission and ensuring continuity of the association from generation to generation (Six 2003).

The fungi associated with bark beetles are primarily Ascomycotina in the Ophiostomatales (*Ophiostoma*, *Ceratocystiopsis*, *Grosmannia*), although a few beetle species carry Microascales (*Ceratocystis*) or Basidiomycotina (*Entomocorticium*). Most bark beetle-fungus symbioses involve multiple fungal partners (Six and Klepzig 2004). The various fungi associated with a host can play redundant or differing roles. For example, the southern pine beetle, *Dendroctonus frontalis*, possesses two nutritional symbionts, *Entomocorticium* sp. A and *Ceratocystiopsis ranaculosus*, which are consistently carried in the beetle mycangium. It also carries an antagonist, *Ophiostoma minus*, loosely on its exoskeleton. *Ophiostoma minus* is a mutualist of *Tarsonemus* mites which are phoretic on the beetles (Lombardero *et al*. 2003; Hofstetter *et al*. 2006a, b). The relative prevalence of each of these fungi has a substantial impact on host population dynamics. Individuals that develop with *Entomocorticium* are larger and have higher lipid contents than those that develop with *C. ranaculosus* (Coppedge *et al*. 1995), and beetle populations with a higher prevalence of *Entomocorticium* exhibit more rapid population growth (Bridges 1983; Goldhammer *et al*. 1990; Coppedge *et al*. 1995). In contrast, as the prevalence of the antagonist, *O. minus*, increases, beetle populations decrease. Indeed, the collapse of outbreaks of *D. frontalis* can be attributed to this fungus reaching a particular threshold of prevalence within trees (Lombardero *et al*. 2003; Hofstetter *et al*. 2006a, b). The prevalence of *O. minus* is directly related to temperature. When temperatures support increases in mite vectors, this increases the prevalence of *O. minus* within the tree relative to the beneficial fungi causing a decline in beetle survival (Lombardero *et al*. 2003; Hofstetter *et al*. 2006a, b).

Importance to ecosystems

The life history of a bark beetle affects how it impacts the ecosystem within which it occurs. Primary beetles are aggressive tree killers capable of developing extensive outbreaks during which most mature host trees in the affected area can be killed (Carroll *et al*. 2004). These insects act simultaneously as pests and as critical natural disturbance agents that maintain the function and structure of the forest ecosystems within which they have coevolved (Raffa *et al*. 2008). For example, the mountain pine beetle develops extensive outbreaks in lodgepole pine and is the primary agent, along with fire, that determines the successional dynamics in lodgepole pine forests (Stone and Wolfe 1996).

In contrast to primary bark beetles, secondary bark beetles are limited to colonizing weakened or dying trees, or trees recently killed by other factors such as fire or wind (Wood 1982). These insects are seldom considered pests and typically act to thin dense tree stands, open gaps enhancing biodiversity, initiate decomposition, and provide food for birds and other wildlife. Extensive outbreaks of these beetles are rare and occur only when large areas of trees become highly stressed, such as often occurs during periods of extended drought or after windthrow, which can provide ample breeding material supporting short-term population increases.

Anthropogenic effects

In many forests, human practices such as logging, removal of preferred species, selective growth of desired species, and fire suppression have led to compositional and demographic changes of host trees. These factors have had considerable impacts on bark beetle distribution and abundance, and consequently, their impacts on forests. For example, fire suppression and some logging practices have led to more expansive areas of susceptible forest than occurred in the past (Taylor and Carroll 2004; Raffa *et al*. 2008). In these forests, the replacement of a mosaic of stands of varying susceptibilities with expanses of homogenous forest now support more extensive bark beetle outbreaks.

In some areas, forest management practices have radically changed the spatial structure and species composition of conifer forests. For example, in the southern US commercial forestry has increased the extent of pine species susceptible to the southern pine beetle while reducing the extent of resistant pines (Perkins and Matlack 2002). Planting practices have also simultaneously increased the connectivity of susceptible pines across the landscape, facilitating more severe and extensive outbreaks of the beetle (Perkins and Matlack 2002). The widespread practice of replanting native forests after harvest or disturbance such as fire, with trees of the same species, but of different geographic origins and genetic makeup, has also likely greatly altered the susceptibility of many forests to bark beetle infestation (Ledig 1992).

Silvicultural practices alter forest structure and composition in ways that affect the beetle-fungus symbiosis as a unit. However, other types of human-caused changes may act to fundamentally alter the symbiosis itself. In the case of climate change, increasing temperatures will affect hosts and symbionts differently, altering the composition, dynamics, and outcomes of the interaction (Six 2009). A spectacular example of how strongly even small changes in temperature can affect an insect-microbe symbiosis, is found in the mountain pine beetle-fungus symbiosis. Responses by the insect partner to temperature are the most obvious and best understood. In recent years, increasing temperatures have resulted in greater survival and productivity, and more rapid development of the beetle (Carroll *et al*. 2004; Régneirè and Bentz 2007; Bentz and Schen-Lagenheim 2007). Warming has allowed rapid expansions of beetle (and fungal) populations as well as remarkable geographic range expansions to the north and east into regions where the beetle did not previously exist (Carroll *et al*. 2004; Lee *et al*. 2007). In the eastern expansion, the beetle is now attacking *Pinus banksiana*

(Jack pine), a species previously not encountered by this insect. Driven by increased temperatures and facilitated by previous land management practices, the current outbreak of mountain pine beetle is now the largest on record for any bark beetle species.

Warming trends are also responsible for recent outbreaks of mountain pine beetle in sub-alpine whitebark pine (*Pinus albicaulis*) forests (Logan *et al*. 2002; Bentz and Schen-Lagenheim 2007; Logan and MacFarlane 2010). Historically, the mountain pine beetle was mostly excluded from the sub-alpine by cold temperatures accompanied by a short growing season. Under these conditions, the beetle underwent a two-year life cycle (Amman 1973). Such an extended life cycle is maladaptive for the mountain pine beetle which would need to survive two winters as well as complete development in a tree dead for 2 years. Under these conditions, mountain pine beetles were excluded, or their populations remained extremely low, in sub-alpine systems. Recently, however, increased temperatures have allowed the beetle to switch to a one-year life cycle in high elevations, which has allowed the development of large populations and rapidly spreading outbreaks. Whitebark pine, a keystone species, is not expected to recover in many areas (Hicke *et al*. 2006; Logan and MacFarlane 2010) with significant cascading effects within the subalpine as well as adjacent ecosystems.

The population dynamics of the mountain pine beetle are strongly influenced by stand conditions and environmental triggers including temperature and drought (Carroll *et al*. 2004). However, dynamics are also likely affected by the beetle's fungal complement. The two mutualistic fungi of the beetle, *G. clavigera* and *O. montium*, like the beetles, are extremely sensitive to temperature, which strongly affects their ability to capture resources (food, space, and hosts), reproduce, and compete with other fungi (Carlile *et al*. 2001). Temperature also strongly affects the relative prevalence of the two fungi with the host beetle (Six and Bentz 2007; Rice *et al*. 2008). Six and Bentz (2007) observed that temperature determines which of the two fungal symbionts is vectored by dispersing adults over a season. *G. clavigera* sporulates in pupal chambers and is acquired in mycangia of newly emerged adults shortly before dispersal when temperatures are relatively cool, while *O. montium* is likewise acquired when temperatures are relatively warm. Temperature may also affect the relative abundance of the fungi over the developmental period of the beetle as strong shifts in the prevalence of the two have been observed from the egg to the adult stage (Adams and Six 2006). These effects are likely to have substantial impacts on beetle fitness by affecting which fungus is predominantly fed upon and dispersed by the beetle. Studies have found that beetles that feed on *G. clavigera* are larger and more fecund than those that feed on *O. montium*. This indicates that when temperatures are cool, this fungus is likely to dominate within the tree, and beetles consequently, are likely to have higher fitness and a higher potential for expanding populations. Likewise, if temperatures are relatively cool during dispersal, *G. clavigera* will be vectored to a greater degree to new host trees.

The stability of bark beetle-fungus symbioses is likely to be affected by warming trends (Hofstetter *et al*. 2006a, b; Six and Bentz 2007). As temperatures rise, this will increasingly select for fungal partners tolerant of warm conditions and against those that require cool conditions. This has a number of ramifications for both symbionts and hosts. In the short term, host fitness is likely to be enhanced or reduced depending upon which symbionts are favored. If a superior symbiont is favored, this should support robust beetle populations with a greater potential for population increase. Conversely, if an inferior symbiont is favored, then the host beetle may become marginalized. Over the long term, increasing temperatures could lead to the loss (and potential extinction) of some symbionts, and consequently, a reduction in the diversity of the symbiont community associated with a beetle (Six and Bentz 2007). Temperature-driven shifts in fungi may also affect population dynamics of the beetles indirectly through effects on natural enemies. Volatiles released by symbiotic fungi are used by some parasitoids to locate their bark beetle hosts (Boone *et al*. 2008; Adams and Six 2008). Therefore, shifts in the relative abundances of fungal associates, or their loss, may influence the degree to which these wasps are able to locate hosts and regulate host populations.

It has been suggested that the individualistic responses of symbionts to environmental conditions, including temperature, may play an important role in maintaining host beetle ecological flexibility. When environmental conditions are unpredictable or variable relative to host generation time, host specialization on one symbiont may not be favored (Baker 2003; Six and Bentz 2007). Under such circumstances, possessing multiple symbionts may aid the host by increasing the probability that at least one symbiont is present (and functional) under prevailing environmental conditions (Six and Bentz 2007). The loss of a symbiont(s) due to altered climatic conditions may, therefore, decrease the ecological flexibility of a host. Ultimately, this may act to restrict its ecological and geographical range to only the conditions under which its remaining symbiont(s) can exist. Finally, new temperature regimes may exclude all symbionts, completely decoupling the symbiosis.

Under climate scenarios predicted for western North America, warming will have serious impacts on the mountain pine beetle-fungus symbiosis. Warming should act to decrease the prevalence of *G. clavigera*, the superior symbiont, and increase the prevalence of *O. montium*, the inferior symbiont. As warming proceeds, *G. clavigera* may be lost from many populations. Indeed, in recent years, mountain pine beetles at sites experiencing hot summers have been observed to carry extremely low levels of *G. clavigera* (Six and Bentz 2007; Bleiker and Six 2008). In addition, aposymbiotic beetles have been collected in areas experiencing very high summer temperatures (Bleiker and Six 2008) indicating that dispersal of *O. montium* will also be reduced as very hot summers become the norm. Aposymbiotic beetles are small and likely have low fitness (Bleiker and Six 2008) indicating that range contractions of the beetle may occur in areas where conditions shift to the point that neither symbiont is supported.

While the thought that mountain pine beetle may be seriously negatively impacted by climate change in the long term may initially give managers a reason to rejoice, it is important to remember that these insects are critical natural agents of disturbance. A change in their role in forest ecosystems could be as undesirable as the effects we are now seeing as a consequence of anthropogenic-induced changes in the occurrence and severity of another important natural disturbance, fire, in western US forests and elsewhere (Keane *et al*. 2002).

Another considerable effect of humans on bark beetle-fungus symbioses is their introduction into novel environments around the globe. Many introduced beetles are likely to exploit the same habitats as native beetles, leading to cohabitation within the same substrate. When this occurs, exotic beetles may encounter fungi associated with native beetles and potentially add these as associates. Conversely, native beetles may acquire exotic fungi from co-occurring exotic beetles. When exotic and native beetles are capable of ‘fungus-swapping’ and have overlapping but different host tree ranges, this can increase the number of tree species exposed to fungi carried by both exotic and native bark beetles. Even when native beetles do not acquire the fungi associated with co-occurring exotics, the fungi associated with exotics may competitively exclude the normal fungal partners of native beetles with potentially serious effects for native biodiversity. While few studies have been conducted investigating these possibilities, there is ample evidence that fungal ‘swaps’ and new acquisitions are occurring (Jacobs *et al*. 2004; Lu *et al*. 2009a, b), as well as evidence in at least one case where an exotic beetle (and potentially its fungal complement) is being competitively displaced by another exotic beetle where the two beetles co-occur (Lee *et al*. 2009).

Given that some bark beetle associates are pathogens, their movement around the world is cause for concern (Wingfield *et al*. 2010). While these fungi do not pose significant threats in their home ranges, they may act differently in new environments and in hosts that have not evolved proper defenses (Brasier 2001). One example where fungal associates may be contributing to a more aggressive behavior of an introduced beetle is that of the red turpentine beetle (*D. valens*). This beetle was introduced into China from North America around 1980. Around 1999, populations of the beetle rapidly expanded and spread across several provinces (Yan et al. 2005). By 2003, over ten million Chinese red pine (*P. tabuliformis*), as well as many other pines had been killed. Isolation studies revealed at least ten species of ophiostomatoid fungi including several from North America, as well as at least one strain from Europe (Q. Lu *et al.* 2008; Lu *et al.* 2009a). The rest were apparently acquired by the beetle in China. Tests revealed that several were pathogens (Lu *et al.* 2009b). At this point, evidence indicates that the fungi alone are not responsible for the aggressiveness of this beetle in China. Rather, it is likely due to a combination of the fungi, a lack of coevolved resistance in the host tree, and drought stress (Lu *et al.* 2009a).

Ambrosia beetle-fungus symbioses

Ambrosia beetles (Coleoptera: Curculionidae, Scolytinae) are close relatives to bark beetles but differ in how they colonize trees and their reliance on fungi as food. Unlike bark beetles, which reside in the phloem and feed on both fungi and tree tissues, ambrosia beetles build gallery systems deep within the sapwood and actively cultivate fungi in 'gardens' as their sole food source (Norris 1979).

Associations between ambrosia beetles and their fungal symbionts are complex and typically involve a community of fungi (Norris 1979; Beaver 1989; Six 2003). The fungi have often been categorized as primary and secondary (or auxiliary) symbionts (Batra 1967). The primary fungi are typically highly consistent with their beetle hosts and are transported in the mycangia of adult beetles (Six 2003). These fungi often predominate in the fungal gardens and provide nutrition for both adults and larvae. Primary fungi occur mainly in the Ascomycotina genera, Ambrosiella and *Raffaelea*, which are closely related to ophiostomatoid bark beetle fungi, but *with* altered morphologies and a complete loss of sexuality (Norris 1979; Blackwell and Jones 1997; Paulin-Mahady *et al.* 2002; Massoumi-Alamouti *et al.* 2009). Secondary fungi are often less consistently associated and, for most, their roles remain unknown (Beaver 1989; Kok *et al.* 1970). One non-ophiostomatoid Ascomycete genus, *Fusarium*, is very commonly isolated from ambrosia beetles. Some *Fusarium* species are primary symbionts while others appear to be secondaries (Norris 1979; Morales-Ramos *et al.* 2000).

Importance to ecosystems

The vast majority of ambrosia beetles colonize trees or woody plants that have been recently killed, or are dying or severely stressed. Through their tunneling actions, they contribute substantially to the degradation of wood and nutrient cycling (Kühnholn *et al.* 2003). Very few species kill healthy trees and ambrosia beetles have not been typically considered pests except when they infest cut logs prior to milling (Beaver and Loyttyniemi 1985; Kühnholn *et al.* 2003).

Anthropogenic effects

One of the major concerns with both climate change and the increasing number of introductions of exotics around the world is the potential for an increase in emerging pests. Ambrosia beetles, which have seldom been thought of as threats to forests in the past, are now at the forefront of concern in this area. In recent years, there have been increasing numbers of reports of ambrosia beetles attacking apparently healthy trees, and together with their fungal symbionts, causing disease and mortality of large numbers of trees (Wood 1982; Bhagwandin 1993; Kamata *et al.* 2002; Kühnholn *et al.* 2003; Coyle *et al.* 2005). A number of hypotheses have been proposed to explain this increase. These include the introduction of beetles into new areas and habitats, effects of climate change on beetle phenology and tree defenses, and changes in fungal symbionts (Kamata *et al.* 2002;

Kühnholn *et al*. 2003). For example, it has been suggested that normally nonpathogenic ambrosia fungi may become pathogenic under conditions of climate change through increasing stress in trees (Kühnholn *et al*. 2003).

The fungi associated with ambrosia beetles have, until recently, not been considered pathogens of trees. However, during the course of the past 10 years, two striking examples have appeared where the primary fungal symbionts of ambrosia beetles have emerged as serious pathogens, resulting in large-scale mortality of apparently healthy trees. These include the disease known as oak dieback in Asia (Kubono and Ito 2002) and laurel wilt disease in the USA (Fraedrich *et al*. 2008). In the case of oak dieback in Asia, it was thought that an exotic fungus was introduced and established a relationship with a native ambrosia beetle, *Platypus quercivora* (Ito and Yamada 1998). Kamata *et al*. (2002), however, rejected this hypothesis and suggested that a more likely explanation is that increased temperatures due to climate change have lead to an expansion of the geographic range of *P. quercivora* bringing the insect into contact with hosts that are more suitable for brood development and susceptible to its associated ambrosia fungus (Kamata *et al*. 2002). In the case of laurel wilt in the USA, the exotic ambrosia beetle, *Xyloborus glabratus*, commonly infests healthy native laurel trees without laying eggs. During these initial infestations, it introduces *Raffaellea lauricola* which is highly pathogenic to laurels. The beetle then disperses but later returns to lay eggs and establish brood galleries once the fungus has compromised tree defenses (Fraedrich *et al*. 2008). The ability to kill healthy trees, in this case, is likely due to the fact that *X. glabratus* and its associated fungus *R. lauricola* have not co-evolved with the tree hosts they infest in the USA and that the tree has little in the way of resistance to the fungus.

The emergence of oak die-back in Asia and laurel wilt disease in the southeastern USA has raised concerns that similar problems might be developing elsewhere. Indeed, a number of new tree disease problems have recently been noted in southern Africa and other parts of the world with which ambrosia beetles and their fungi are involved. The ambrosia beetle, *Megaplatypus mutatus*, for example, kills *Populus* in South America (where the beetle is native but the tree is not) and Italy (where the tree is native, but the beetle is not) (Alfaro *et al*. 2007). Likewise, mortality of native *Taeberna montanum* trees in South Africa has been found to be associated with infestation by an exotic ambrosia beetle, *Xylosandrus crassiusculus*, which carries *A. beaveri* in this location (Roux *et al*. 2010). Interestingly, the exotic ambrosia beetle, *X. mutilatus*, carries *A. beaveri* in the southeastern US, but in this case, the beetle is limited to stressed, dying or dead material (Stone *et al*. 2007; Six *et al*. 2009). The threat to native forests from exotic ambrosia beetles and their fungi cannot be underestimated. Ambrosia beetles and their symbionts are among some of the most easily and commonly introduced forest insects in the world. They are typically minute, buried deep within wood xylem, and thus, are easily transported in timber and wood-based packaging material (Haack 2001; Mireku and Simpson 2002). The relative ease with which these beetles can be transported long distances is complimented by the fact that many of the beetles, as well as their fungi, are polyphagous, increasing their chances of finding suitable hosts once introduced into a new environment. Furthermore, the breeding strategies of ambrosia beetles are highly conducive to establishment. Many ambrosia beetles are inbreeding and so do not face problems with mate location or inbreeding depression, and can potentially start a new population from a single fertilized female (Kirkendall 1993; Normark *et al*. 1999).

Sirex-fungus-nematode symbioses

Siricids that attack conifers (Hymenoptera: Siricidae) are obligately associated with fungi in the genus *Amylostereum* (Basidiomycotina) (Morgan 1968; Slippers *et al*. 2003). In most cases, the wasp provides transport and protection for the fungus in internal mycangial sacs associated with the ovipositor of adult female wasps and in external mycangial pockets of the larvae (Talbot 1977). The female wasp introduces the fungus into the wood, together with her eggs, after drilling through the bark with her saw-like ovipositor. At this point, the wasps also introduce a phytotoxic mucus that affects the defense mechanisms of the tree which is important for the establishment of both the wasp and the fungus (Coutts 1969). Only one genus of Siricidae, *Xeris*, do not have mycangia, but rather infect wood that has previously been colonized by *Amylostereum* following attack by other siricids or wounding (Fukuda and Hijii 1997). The fungus is thought to facilitate the tunneling of developing wasp larvae by physically softening the wood by causing white-rot. The larvae are also thought to gain nutritional benefit from the fungus, both indirectly through the decomposition of cellulose into compounds usable by the insects, and directly by ingestion of the fungal hyphae (Madden and Coutts 1979; Kukor and Martin 1983).

Siricids and their mutualistic fungi are parasitized by nematodes in the genus *Deladenus* (=*Beddingia*) (Bedding and Akhurst 1978; Bedding and Iede 2005). These nematodes have a bi-cyclic life cycle. In one phase, they are morphologically adapted to feed on the *Amylosterum* symbiont (mycetophagous phase), while in the second, they are adapted to penetrate, feed upon, and reproduce in the larvae of the wasps (parasitic phase). Different species of nematodes are obligate on specific *Amylostereum* species during their mycetophagous phase (Bedding and Akhurst 1978; Bedding and Iede 2005). They infect both male and female siricids, but are only spread by females during egg-laying. The nematodes also infect wasps parasitic on siricids, but their ability, if any, to spread in these insects is not known.

Importance to ecosystems

Siricids are native to the Northern Hemisphere where most species attack mature, dying, or recently killed trees (Spradbery and Kirk 1978). As such, they contribute to tree succession and the decomposition process. One exception is *Sirex noctilio*, a Eurasian wasp that frequently attacks living trees, although predominantly those that are severely stressed. This species has rarely been viewed as a serious threat to forests or plantations of pine in its region of origin. In contrast, *S. noctilio* has caused serious damage to pine plantations in the southern hemisphere where it has been accidentally introduced several times (Neumann and Minko 1981; Haugen 1990; Hurley *et al.* 2007). In the Southern Hemisphere, up to 80% mortality has been recorded in outbreaks in plantations. The difference in the impact of this insect in areas of introduction compared to in its native range has been attributed to the absence of, or irregular pressure from, natural enemies, the presence of large stands of susceptible hosts that are uniform in age and genetic composition, and wide-scale stress in host trees (either due to poor management, dense planting practices, or natural environmental factors such as drought) (Neumann and Minko 1981; Haugen 1990; Hurley *et al.* 2007).

Anthropogenic effects

The movement of wood around the world by humans has resulted in the successful establishment of *S. noctilio* on several continents. The first establishment of this insect and its *Amylosterum areolatum* symbiont outside its native range was in New Zealand around 1900 (Hurley *et al*. 2007). The wasp subsequently spread to Australia, various South American countries, South Africa, and, most recently, North America (Hoebeke *et al*. 2005; Nielsen *et al*. 2009). Prior to its introduction to North America where the insect is now established in native forests, all introductions were into plantations of exotic pines.

The movement of *S. noctilio* around the world has resulted in a number of changes in wasp behavior, as well as in the wasp-fungus symbiosis. Despite the fact that *S. noctilio* is not a pest in its home range, when it first appeared in Australia the damage in plantations was sufficiently severe to justify a major program to manage the insect (Neumann and Minko 1981; Madden 1988). A key component of this program was biological control using introduced parasitoid wasps and the *Sirex*-

specific parasitic nematode, *Deladenus siricidicola*, strains of which were introduced from various parts of the home range of the wasp (Bedding and Akhurst 1978; Bedding and Iede 2005).

Of all the biological control agents used to manage populations of the wasp, *D. siricidicola* has been the most fundamental (Bedding and Iede 2005; Hurley *et al*. 2007), yet efficacy has been variable. For example, in Australia, extensive inoculation programs in the 1980 s eventually failed when the nematode lost its virulence (Haugen 1990, Haugen and Underdown 1993). The loss of virulence was resolved by introducing a newly isolated strain, Kamona, from Tasmania (Bedding and Iede 2005). However, the Kamona strain was not equally effective in all cases. For example, in South Africa, the expectation was that the nematode would provide a rapid solution to a sizeable outbreak of the wasp that recently occurred in the major pine-growing areas of the country. However, only poor levels of success were achieved (Hurley *et al*. 2007; 2008). Although the basis of this problem remains to be fully resolved, various factors relating to the symbiosis between the wasp, its fungal associate and its parasitic nematode have emerged. For example, it was found that the genotype of *A. areolatum* on which the Kamona strain of *D. siricidicola* is raised is different to that associated with wild populations of the wasp in South Africa (Slippers *et al*. 2002; 2003). The Kamona strain of the nematode from Australia grows less effectively on the strain of *A. areolatum* carried by *S. noctilio* in South Africa under some conditions (BP Hurley, B Slippers, unpublished data) which may account, at least in part, for the low infection rates achieved in that country thus far.

The success of both the wasp-fungus symbiosis and biological control programs for its control using the parasitic nematode depend on a complex suite of environmental conditions (Hurley *et al*. 2007; 2008). For example, the moisture content of *Sirex*-infested wood is crucial to the development of *A. areolatum*, and thus, *D. siricidicola*. Therefore, climate will strongly influence the wasp, its symbiont and its biological control agents, each of which will respond in an idiosyncratic manner. As conditions change due to global warming, the relative suitability of an environment for each will also change with subsequent effects on the ability of the wasp to kill trees and also the efficacy of biological control.

Competition with other organisms is also likely to influence the biology of the wasp, itsmutualistic fungus, and its parasites. For example, in South Africa, *S. noctilio*-infested trees are rapidly colonized by the exotic European bark beetle, *Orthotomicus erosus*. *Orthotomicus erosus* carries a symbiotic fungus, *O. ips*, which colonizes the wood. In addition, trees are often colonized by *Diplodia pinea*, a fungus that is either endophytic in the tree or that is also introduced by the bark beetles (BP Hurley, B Slippers, unpublished data). Competition for resources likely occurs between the *S. noctilio* symbiont, *A. areolatum* on which *D. siricidicola* and the wasp must feed, and the bark beetle fungal symbiont(s) that require(s) the same wood resources for their growth and survival. The outcome of this competition under changing environmental conditions likely influences the relative success of S. noctilio at a given site over time.

The recent invasion of *S. noctilio* in North America presents a very different situation from introductions into the Southern Hemisphere because this is the first area where the wasp has appeared as an exotic where pines are native (Hoebeke *et al*. 2005; Nielsen *et al*. 2009). As an exotic in North America, *S. noctilio* will encounter native siricid wasps, their fungal symbionts, and their natural enemies. It will also encounter bark and ambrosia beetles with their complements of fungi. It is unclear how native wood wasp-fungus-natural enemy and bark- and ambrosia beetle-fungus complexes will interact with *S. noctilio* and its fungus, but it is likely that the wasp and its symbiont will compete for resources very differently in these forests than it has in plantations of non-native pines in the Southern Hemisphere, which to a large extent represent an open niche that the wasp has been able to fill.

Sirex noctilio is an interesting case where we have a symbiosis occurring under multiple unique situations: as a native in native hosts in its native environment, as an exotic in exotic hosts in an exotic environment, and as an exotic in native hosts in an exotic environment. In the various regions where this insect is established, the symbiosis also experiences a variety of climate regimes including winter, summer, and bimodal rain patterns as well as different competitors. This provides us with the unique opportunity to investigate, for one symbiosis, how changes in the environment, whether natural or anthropogenic, can affect outcomes.

Fungus-growing ant-microbe symbiosis

Ant-fungus symbioses occur among more than 200 described species of ants in the tribe Attini (Hymenoptera) and the fungi (Agaricales: Lepiotaceae, Pterulaceae) they cultivate for food (e.g., Weber 1966; 1972). While several distinct strategies of ant-fungus agriculture occur within this broad form of symbiosis (Schultz and Brady 2008), the leaf-cutting ants (genera *Atta* and *Acromyrmex*) have evolved the ability to harvest and use fresh plant material for maintaining their fungus cultivar. Along with two other genera (*Trachymyrmex* and *Sericomyrmex*), leafcutting ants practice what has been termed 'higher agriculture'. In higher attine agriculture, the cultivated fungus no longer appears to be able to exist outside the mutualism. These fungi have evolved specialized gongylidia, nutrient-rich hyphal swellings, which are harvested by the ants and used to feed primarily to ant larvae (Chapela *et al*. 1994; Mueller *et al*. 2001).

In attine agriculture, there are four microbial symbionts that form an integrated part of the fungus-growing ant-microbe symbiosis. These include the mutualistic fungus that the ants maintain for food (Möller 1893; Hölldobler and Wilson 1990) and fungi in the genus *Escovopsis* that parasitize the ants' mutualistic fungus. *Escovopsis* have been shown to directly target and consume the beneficial fungus (Currie *et al*. 1999a; Reynolds and Currie 2004) and appear to be specific to attacking fungus-growing ant-associated fungi. They are associated with the majority of fungus-growing ants, and can incur significant fitness costs to ants in infected nests (Currie 2001; Currie *et al*. 2003a, Poulsen *et al*. 2010) and can devastate entire colonies (Currie *et al*. 1999a; MP, personal observation). In addition to employing behavioral defenses to physically remove *Escovopsis* from infected garden material (Currie and Stuart 2001; Abramowski *et al*. 2011), the ants employ defensive mutualists to control *Escovopsis*. These are *Pseudonocardia* bacteria (Actinomycetales: Pseudonocardiaceae) (Currie *et al*. 1999b; Cafaro and Currie 2005) that are maintained on the cuticle of the ant host where they secrete secondary metabolites that strongly inhibit *Escovopsis* (Currie *et al*. 2006; Oh *et al*. 2009; Poulsen *et al*. 2010; Cafaro *et al*. 2011). Experiments where *Pseudonocardia* has been removed have resulted in subsequent *Escovopsis* infection (Currie *et al*. 2003a). Likewise, a recent evaluation of the role inhibitory properties of *Pseudonocardia* play in regulating *Escovopsis*-induced morbidity (Poulsen *et al*. 2010) supports the hypothesis that the ants use antibiotics from *Pseudonocardia* to limit *Escovopsis* infections.

Despite decades of work on the fungus-growing ant system, recent work has identified two additional symbiont groups. The first is black yeast (Ascomycota; Phialophora) that grows on the same locations on the ant cuticle as *Pseudonocardia* (Little and Currie 2007) and appears to exploit the fungus-growing ant system by acquiring nutrients from *Pseudonocardia* thereby reducing its ability to suppress *Escovopsis* (Little and Currie 2008). Furthermore, nitrogen-fixing bacteria (*Klebsiella* and *Pantoae*) are also present within fungus gardens of leafcutting ants. These bacteria fix atmospheric nitrogen in the fungus garden and, as the ants consume the fungus material, the fixed nitrogen becomes incorporated into the ants (Pinto-Tomás *et al*. 2009).

Fungus-growing ants, the cultivar fungus, the parasites of the fungus, and the defensive *Pseudonocardia* mutualists have all undergone some degree of co-diversification, and possibly coevolution (Mueller *et al*. 1998; Currie *et al*. 2003b; Cafaro *et al*. 2011). The two best-studied mutualistic symbionts, the cultivar and *Pseudonocardia*, are both vertically transmitted between host-ant generations by default (von Ihering 1898; Autuori 1956; Currie *et al*. 1999b; Mueller *et al*. 2001; Fernández-Marín *et al*. 2004), leading to expectations of patterns of host-mutualist cocladogenesis, which indeed is observed. Despite default horizontal transmission between nests (Currie *et al*. 1999a), *Escovopsis* also show some degree of broad-scale congruence with the ants and host cultivars (Currie *et al*. 2003b). Thus, patterns of phylogenetic congruence between the ants and their associated symbionts are characterized by broadscale phylogenetic matching creating distinct groups of ants and associated symbionts. Within these groupings, switching of symbionts within and between ant species, and genera, appears to be frequent, disrupting strict patterns in lower-level phylogenetic congrunce (Adams *et al*. 2000; Poulsen *et al*. 2005; Taerum *et al*. 2007; Gerardo and Caldera 2007; Mikheyev *et al*. 2007, Poulsen *et al*. 2009).

Importance to ecosystems

Leaf-cutting ants are major herbivores in tropical New World forests and agricultural landscapes (Hölldobler and Wilson 1990). Workers from individual mature *Atta* leafcutter nests and can harvest more than 200 kg dry weight of leaf material per year (Wirth *et al*. 2003), and consequently, they play a major role in nutrient cycling in tropical forests. They may also play an important role in nitrogen cycling due to their association with nitrogen fixing symbiotic bacteria (Pinto-Tomás *et al*. 2009). In addition, leaf-cutting ant colonies, through deposition of seeds in their dumps, can play a significant role in seedling recruitment during the dry season (Farji-Brener and Ghermandi 2004). Although less is known about the ecological role and impact of the lower attines, at least one study has documented a beneficial effect of these ants in dispersal of seeds from non-myrmecophyte plants (Leal and Oliveira 1998).

Anthropogenic effects

There has been little focus on anthropogenic effects on fungus-growing ants, likely because the most conspicuous fungus-growers, the leaf-cutting ants, appear to be resilient to the most obvious direct influences of humans on forest ecosystems, deforestation and habitat fragmentation (Mayhé-Nunes and Jaffe 1998). However, studies examining habitat use by fungus-growing ants indicate that human-caused changes in habitat may have significant impacts. Certain genera are plastic in habitat use (lower attine species in the genera *Cyphomyrmex*, *Mycetarotes* and *Mycetosoritis*, and the higher-attine genera *Trachymyrmex* and *Sericomyrmex*,), while some genera are highly specific (the lower attine genera *Mycetophylax* and *Mycocepurus*) (Mayhé-Nunes and Jaffe 1998). Consequently, different habitats harbor distinct, but overlapping, attine species compositions. As habitats are altered due to logging, clearing for agriculture, or climate change, such alterations are likely to induce changes in ant species composition (cf. Vasconcelos *et al*. 2008) impacting ant species diversity through either species composition changes and/or species loss.

Ant symbiont communities are expected to follow changes in ant communities. However, some may shift in response to environmental change with subsequent alterations of natural host-mutualist dynamics. This is because, despite default vertical transmission, there is frequent between-colony switching of both the fungal cultivar and *Pseudonocardia* mutualists. Ecological and geographic range shifts due to climate change may, therefore, result in losses of some symbionts as well exposure to new ones. Similarly, the association with *Escovopsis* is shaped by host switching within and between ant species, so that changes in ant abundance and community composition has the potential to alter what hosts are available, and hence, alter host-parasite dynamics.

In addition to the direct effects of anthropogenic change on fungus-growing ant species, diversity, abundance, and symbiotic associations, there are several potential indirect effects. Leaf-cutting ants play several major roles in New World tropical forest ecosystems. They harvest large amounts of vegetation affecting the demography of individual plants and the structure and composition of the plant community as a whole. Through their fungal gardens, they accelerate the decomposition process, thus shortening nutrient cycling times (Fowler *et al.* 1989). Studies exploring plant community successional patterns suggest that leaf-cutting ants nests may be focal points for ecosystem renewal and promote increased plant diversity (Fowler 1977; Jonkman 1978). Several vertebrates and many invertebrates are also dependent in one way or another upon the ants and their nests (Weber 1972). Because substrate use differs between species, changes in leaf-cutting ant species distribution will likely affect plant species distributions and nutrient flow (Fowler *et al.* 1989). Consequently, changes in plant diversity, species abundances, and community composition are expected due to anthropogenic effects on ant distribution. Furthermore, nitrogen fixation by symbionts associated with leaf-cutting ants may play an important role as a nitrogen source in tropical ecosystems (Pinto-Tomás *et al.* 2009), implying that a reduction or turnover in species composition of ants in an area has the potential to alter nitrogen flow.

Termite-fungus symbioses

The termite-fungus mutualism occurs between members of the termite subfamily Macrotermitinae (Termitidae) and fungi in the genus *Termitomyces* (Basidiomycotina) (Aanen and Boomsma 2006). Termite workers build a soil structure within which the colony and symbiotic fungus is housed. In some cases, these structures are entirely below-ground, but for the most complex group (genus Macrotermes), the structures consist of large architecturally complex mounds (Darlington and Dransfield 1987). These mounds act not only to protect the fungal symbiont, but also to protect and defend the termites, and in extreme cases, the mound acts as a form of lung, allowing gas exchange between the colony members and the atmosphere (Turner 2001).

The fungus retains a full sexual cycle with fruiting bodies (mushrooms) that push up through the walls of the mound to erupt above the soil surface. These fruiting bodies produce basidiospores which are dispersed into the environment, often onto the soil surface surrounding the mound (Aanen *et al.* 2002). In nearly all macrotermitine species, these spores are picked up by foraging workers from a recently established termite colony and taken back to the nest. Within the nest, the spores are mixed with partly-digested dead plant material (wood, leaf litter or grass) to form a fungus comb. The comb is expanded over time and becomes the site of the majority of the digestive activity within the nest and provides food for the entire colony. *Termitomyces* is able to break down both cellulose and lignin in dead wood, thus the digestion of plant material placed into the comb and its conversion to fungal comb (and respiratory gases) is very close to complete (Ohkuma 2003; Konate *et al.* 2003). This relationship appears to have evolved in the early Tertiary within African megathermal forest. Subsequently, the mutualist system has colonized Asia and Madagascar, but is absent from the New World, Europe and Australia (Aanen and Eggleton 2005).

Importance to ecosystems

Fungus-growing termites are distributed in four main broad habitats: rainforest, forest edge, wet savannas and dry savannas and do not penetrate far into drier or colder habitats (Aanen and Eggleton 2005). There is considerable species turnover between these habitats, but with species richness and generic richness declining as rainfall declines (Eggleton 2000). In contrast, the ecological impact of fungus-growing termites is probably hump-shaped with the greatest impact occurring in savannas with intermediate levels of rainfall where they are undoubtedly the most important decomposer organisms (Schuurman 2005). Fungus-growing termites are key ecosystem engineers, strongly affecting a wide range of soil properties and vegetation. They can collect up to 60% annually of the grass, wood and leaf fall in an area. This acts to reduce fuel loads and fire intensity while simultaneously enriching soil (Jones 1990; LePage *et al.* 1993). Termites, their fungi, and their mounds, also provide shelter and food for many organisms occurring within and around their mounds (Sileshi *et al*. 2009; Pringle et al. 2010). These include numerous arthropods, as well as many vertebrates including birds, reptiles, aardvarks, chimpanzees and gorillas (Sileshi *et al*. 2009). Humans also utilize termite mound soil and consume *Termitomyces* mushrooms (Sileshi *et al*. 2009).

Anthropogenic effects

The ecological function of fungus-growing termites is generally less susceptible to anthropogenic conversion of rainforest to derived savannas than are other termitid groups. This is because macrotermitines from surrounding habitats often invade disturbed areas including areas developed for agricultural use where they can become pests (Wood *et al*. 1980). However, whether this occurs or not depends partly on the species present and partly on how isolated undisturbed habitat blocks are from one another. In southern Cameroon, forest disturbance causes a decline in diversity with no compensating influx of savanna species. In contrast, in some areas where macrotermitines persist after disturbance, they can become the dominant termites. For example, in Malaysia, the forest edge specialist, *Macrotermes gilvus*, reaches very high densities in oil palm plantations (P. Eggleton, personal observation).

Conversion of natural systems into agricultural land often leads to an increase in the impact of pest fungus-growing termite species, typically savanna-specialists that are likely to have had a long evolutionary association with humans (Wood 1996). These include timber pests, which are found in all habitats, and crop pests, which are particularly prevalent in cleared areas. In Africa, particular pest genera are known to specialize on different parts of the crop plant, including roots, stem and leaves (Wood, 1996).

Because fungus-growing termites can be pests, this has led to efforts to control them in some situations. Organochlorine compounds were used commonly until banned due to adverse environmental effects. The focus now is on the use of fungicides that target the *Termitomyces* symbiont (Rouland-Lefevre and Mora 2002). However, the control of fungus-growing termites may negatively affect humans and non-target organisms, soil productivity and ecosystem services, and traditional human cultural linkages to the termites and *Termitomyces* (Sileshi *et al*. 2009).

The ecological consequences of forest disturbance and fragmentation are clear for termites as a whole: functional diversity is reduced considerably in fragmented and disturbed rainforest areas and diversity is lower in savannas than in rainforests (Davies *et al*. 2003). This applies particularly to soil-feeding termites, which provide essential ecosystem services in the soil (Donovan *et al*. 2001). However, this pattern is not so evident in fungus-growers, as they show greater resilience and complementary species turnover than most other termite groups. The considerable decompositional services that they provide are, therefore, less attenuated across a disturbance gradient and/or a forest—savanna one (Wood and Sands 1978).

Climate change is predicted to make most tropical environments hotter and drier. This will likely reduce macrotermitine diversity, but potentially increase the relative ecological impact of the fungus-termite mutualism, overall. Drier areas will have fewer free-living fungal decomposers, and so *Termitomyces* is likely to be at a selective advantage. This advantage, however, will only occur where reductions in rainfall are not too great, as areas converted to semi-deserts or deserts will be too dry to support fungus-growing termites and their fungi. Besides effects on soils and decomposition, cascading effects of these changes are expected to affect the may organisms that habitually co-exist with macrotermitines (Pringle *et al*. 2010).

Hemiptera-bacteria symbioses

Most hemipterans possess bacterial endosymbionts that are either obligate or facultative for survival and reproduction (primary and secondary endosymbionts, respectively) (Buchner 1965; Baumann *et al*. 2005; Moran *et al*. 2008; Oliver *et al*. 2010). Many primary endosymbionts are enclosed in host-derived vesicles (bacteriocytes) and are widespread in hemipterans that feed on nutrient-limited diets, such as plant sap (Buchner 1965; Baumann *et al*. 2005). The benefit of primary symbionts to their hosts is thought to be nutritional and has been extensively studied in the bacterial symbiont *Buchnera* and its aphid (Aphidae) hosts (Baumann *et al*. 1995; Shigenobu *et al*. 2000; Sandström *et al*. 2001; Moran *et al*. 2005).

In contrast to primary symbionts, secondary symbionts are not harbored within specialized cells, but rather occur within their host's hemolymph, glands, gut tissue, sheath cells surrounding the primary symbionts's bacteriocytes, or syncytial tissue surrounding bacteriocytes (Buchner 1965; Fukatsu and Nikoh 1998; Fukatsu *et al*. 2000; Subandiyah *et al*. 2000; Mira and Moran 2002). The effect of secondary symbionts on their insect hosts are not well understood (Baumann *et al*. 2000; Baumann 2005); however, in the *Acyrthosiphon pisum* (Hemiptera: Aphidae) system, they are known to exert a number of effects including resistance to parasitoids (Oliver *et al*. 2003; 2005; Ferrari *et al*. 2004; Vorburger *et al*. 2010) and fungal entomopathogens (Ferrari *et al*. 2004, Scarborough *et al*. 2005), thermal tolerance (Chen *et al*. 2000; Montllor *et al*. 2002; Russell and Moran 2006), and host plant specialization (Tsuchida *et al*. 2004).

Importance to ecosystems

The order Hemiptera is one of the most ecologically diverse orders of all insects (Gaston 1991; Cassis and Gross 1995; Moir and Brennan 2007). In forest habitats, Hemiptera occupy multiple trophic levels and microenvironments. The vast majority of hemipteran species are known to be plant feeders; however, carnivorous, omnivorous, and fungivorous species are also common (Moir and Brennan 2007). Forest hemipterans occupy multiple forest microhabitats including the understory (soil, leaf litter, roots, under logs and rocks) and the overstory (colonizing a wide variety of plant micro-habitats including leaves, stems, petioles, buds, bark, flowers, and galls) (Schowalter and Zhang 2005; Moir and Brennan 2007).

Hemipterans play important roles in forest foodwebs. They provide abundant prey for many invertebrate and vertebrate forest predators (Moir and Brennan 2007). Additionally, some herbivorous species exhibit outbreak dynamics in forest ecosystems and consequently influence plant community composition and structure (Hill 1947; White 1971; Morgan 1984; Yukawa 1984; Wylie and Peters 1993) and forest successional trajectories and disturbance dynamics (Moir and Brennan 2007).

Anthropogenic effects

Numerous hemipterans have become invasive pests in natural forests, plantations, urban forests, and agriculture because of accidental human introductions. The potential for successful establishment of an exotic organism is typically attributed to propagule pressure, ability to survive and increase from low densities, and intrinsic as well as extrinsic factors that determine population abundance (Williamson 1996). In the case of several invasive hemipterans, secondary bacterial endosymbionts have also played important roles in increasing the likelihood of their host's success in new environments by modulating their interactions with natural enemies (Oliver *et al*. 2003; Oliver *et al*. 2006; Hansen *et al*. 2007; Vorburger *et al*. 2010) and inducing thermal tolerance (Chen *et al*. 2000; Montllor *et al*. 2002; Russell and Moran 2006; Dunbar *et al*. 2007; Harmon *et al*. 2009).

Microbial symbionts can influence biological control efforts to manage invasive hemipterans. For example, the pea aphid, *A. pisum*, a native to Eurasia, was first detected in North America in the 1870 s (Harper *et al*. 1978). In the 1960 s, a parasitoid wasp, *Aphidius ervi*, was released to control the aphid (Halfhill *et al*. 1972; Mackauer and Campbell 1972; Angalet and Fuester 1977). It was soon noted that different clonal lines of *A. pisum* varied in susceptibility to the parasitoid (Henter and Via 1995). This variation was initially thought to be caused by genetic variation in the aphid host's genotype (Henter and Via 1995); however, subsequent laboratory studies revealed that secondary endosymbionts (*Serratia symbiotica*, *Hamiltonella* defense and *Regiella insecticola*) may in fact be the primary factors conferring resistance to the wasp (Oliver *et al*. 2003; Vorburger *et al*. 2010). The genetic mechanism involved in *H. defensa* induced-resistance, for the strain that confers the greatest resistance toward the parasitoid, is linked to a lysogenic lambdoid bacteriophage, APSE (Moran *et al*. 2005; Degnan and Moran 2008, Degnan *et al*. 2009; Oliver *et al*. 2009).

Indirect evidence of symbiont-induced resistance toward a parasitoid has been found in the exotic red gum lerp psyllid, *Glycaspis brimblecombei* (Hansen *et al*. 2007). This psyllid invaded California from Australia where it became well established on an important introduced urban forest tree, *Eucalyptus camaldulensis* (Paine *et al*. 2000). In 2001, the parasitoid, *Psyllaphaegus bliteus*, was released to control the psyllid (Paine and Millar 2002). This parasitoid is a specialist of *G. brimblecombei* in its native range in Australia where it is important in regulating psyllid populations (Dahlsten *et al*. 2005). After release, successful establishment and population regulation by *P. bliteus* was found in some psyllid populations, but not in others (Dahlsten *et al*. 2005). A subsequent survey found that infection frequencies of a secondary endosymbont (*Arsenophonus* sp.), varies dramatically among psyllid populations, and is significantly related to wasp parasitism pressure. Collectively, these results suggest that resistance is induced by the symbiont (Hansen *et al*. 2007). Interestingly, the psyllid's *Arsenophonus* secondary endosymbiont encodes for an APSE-like phage gene within the bacterium's chromosome which shares >90% similarity to the APSE polymerase gene from the lytic phage associated with *H. defensa*-induced resistance in the pea aphid (Hansen *et al*. 2007). This phage is incorporated into the chromosome of *Arsenophonus*; however, and does not appear to be lysogenic or lytic (Hansen *et al*. unpublished data).

Insects have restricted thermal tolerances. Therefore, a very important factor for the establishment of an exotic species is climate matching. In *A. pisum*, it has been found that *S. symbiotica*-infected clones have higher fitness relative to un-infected clones during heat shock treatments in the lab (Chen *et al*. 2000; Montllor *et al*. 2002; Russell and Moran 2006). It has also been found that a mutation in the promoter region of a heat-shock gene in *A. pisum*'s primary endosymbiont (*Buchnera*) can influence heat tolerance (Dunbar *et al*. 2007). Using field cages, Harmon *et al*. (2009) found that aphids harboring the active *Buchnera* promoter and *S. symbiotica* exhibited greater population increase under hot conditions relative to aphids harboring the impaired *Buchnera* promoter and which were uninfected with *S. symbiotica*.

Field studies have found that infection frequencies of *A. pisum* by *S. symbiotica* can reach up to 80% in warm habitats such as in the Central Valley of California where the insects have become major pests (Chen and Purcell 1997). Moreover, *S. symbiotica* strains obtained from colder environments conferred less of a fitness benefit in the lab during heat shock treatments relative to a strain from a warmer location (Arizona) (Russell and Moran 2006). Nevertheless, all strains conferred higher fitness to their hosts during heat shock relative to un-infected *A. pisum* clones (Russell and Moran 2006). These results suggest that the ability of the pea aphid to tolerate a broad range of thermal conditions in its invasive range is mediated and supported by its endosymbionts, contributing to its establishment and spread.

The introduction of exotic hemipterans has had serious implications for both native and exotic plantation trees and urban forests around the world, typically through feeding damage by these often prolific breeders. Coversely, the introduction of exotic crops and trees has provided opportunities for native hemipterans that were not previously pests to become pests as they switch onto new and economically important host plants. One reason why some native hemipterans become major pests on exotic plants is because of their intimate interactions with bacterial endosymbionts (Hosokawa *et al*. 2007; Hansen et al. 2008; Bressan *et al*. 2009), which can mediate their success on the new host or even act as pathogens. While examples of such switches are rare for forest systems, examples from agriculture abound. Such effects are likely to increase as plantation and urban forests composed of exotic species continue to expand worldwide.

One example of where symbionts have supported a host shift by a native hempiteran onto an exotic plant has been observed in Japan. In this case, two geographically isolated plataspid stinkbugs, *Megacoptera punctatissima* and *M. cribraria*, which feed on two native leguminous vine host plants, *Pueraria lobata* and *P. montana*, respectively. Each stinkbug harbors an obligate primary endosymbiont, *Ishikawaella capsulata*, which is vertically transmitted externally as a 'symbiont capsule' under the egg mass. Once nymphs hatch they orally acquire the symbiont from the capsule. Hosokawa *et al*. (2007) found that when they switched egg mass capsules between the species their performance on soya bean plants and pea pods were completely reversed. These results suggest that the pest status of *M. punctatissima* is determined solely by its primary symbiont and not by insect genotype.

Human introductions of exotic plants can also influence vectoring of disease by native hemipteran insects. Interestingly, bacterial endosymbionts can also sometimes act as pathogens when injected by the insect into a plant. The syndrome 'basses richesses' (SBR) is a phloem-restricted disease of sugar beet (*Beta vulgaris*) in eastern France, and is associated with a SBR bacterium that is vectored by the planthopper, *Pentastiridius leporinus* (Bressan *et al*. 2009). Additionally, a closely related bacterium, *Phlomobacter fragariae*, is the main causal agent of marginal chlorosis disease of strawberry in western France and is vectored by the cixiid planthopper, *Cixius wagneri*. Both bacteria reside within the *Arsenophonus* clade (Bressan *et al*. 2009; Nováková *et al*. 2009). Interestingly, *Arsenophonus* species are primarily known as insect endosymbionts and not as plant pathogens (Gherna *et al*. 1991; Hansen *et al*. 2007; Allen *et al*. 2007; Trowbridge *et al*. 2006; Perotti *et al*. 2007). The plant pathogen, SBR, appears to be intimately associated with its insect host since it is vertically transmitted, is maintained throughout all planthopper life stages, and is found in planthopper gonads, salivary glands, gut, bacteriomes, and malpighian tubules (Bressan *et al*. 2009). Whether or not the bacterium increases its insect vector's fitness on diseased crop plants remains to be determined. Another bacterium with a duel role as an endosymbiont and plant pathogen is *Liberibacter psyllaurous*, which is harbored by the tomato psyllid *Bactericerca cockerelli* (Hansen *et al*. 2008).

Topics for future research

Climate change

Climate change will increasingly affect symbioses including mutualisms, and unlike for most other anthropogenic effects, changes in on-the-ground policy or management, or the implementation of strategic measures to alleviate impacts, in most cases, cannot be used effectively to lessen its impact. With emissions of carbon dioxide and other greenhouse gases continuing to increase, effects will not only continue but become increasingly severe.

Mutualisms, particularly those occurring between ectotherms such as those showcased in this review, are particularly sensitive to changes in temperature. They retain stability and function under one set of conditions but may decouple as conditions shift beyond the particular thresholds of one or more partners. Such effects are not trivial. Effects on key mutualisms will likely ramify throughout ecosystems with as-of-yet unknown outcomes. In order to better understand how climate change will affect ecosystems, we will need to incorporate these critical interactions into the conceptual and predictive models we use to guide our research and conservation goals. For example, phenological models for the host are often used to predict range expansions and contractions under various climate scenarios. However, the use of phenological models for both hosts and symbionts in tandem will generate more accurate predictions of such range changes by detecting where critical symbionts may become marginalized or lost. While the use of host and symbiont models together will be a significant step forward in understanding the response of mutualisms to warming trends, this approach does not incorporate the potential for the host or its symbionts to adapt to rapid warming or to switch partners as thermal regimes change. To understand if adaptation or partner switching is likely, we will also need to begin to assess levels of heritable variability and phenotypic plasticity to different scenarios, as well as experimentally challenge hosts and symbionts with potential new partners and to increased temperatures in controlled experiments.

Forest insect-microbe mutualisms provide some of the most amenable and appropriate systems to study for effects of climate change on mutualisms. They have significant impacts on the ecosystems within which they exist and information on their response to changing temperature regimes is needed to predict future conditions in our forests. The organisms involved are small in size and rapid to respond to even small changes in environmental conditions. Furthermore, forests often span significant latitudinal and elevational gradients allowing us to study particular symbioses under different environmental conditions and in areas undergoing differing degrees of climate change.

Exotic introductions

The introduction of exotic insects is one of the biggest threats to forest ecosystems. The movement of wood and wood products is one of the biggest contributors to the movement of exotic insects globally. Wood-boring insects feed on nutritionally poor substrates and depend on microbial endo- or ectosymbionts to aid in breaking down cellulose and lignin, to provide sterols, vitamins, and other critical compounds, or to concentrate or fix nitrogen. While many of these microbial partners pose no threat, some are pathogens and exhibit greater pathogenicity in new environments and host trees than in their native range. Therefore, not only the effects of the exotic insect must be considered when attempting to predict negative impacts of establishment, but also the impact their symbionts may have when introduced into tree hosts with which they have not coevolved. Unfortunately, it can seldom be predicted which symbionts will exhibit virulence in novel tree hosts. Currently, it is only after introduction that such effects become apparent. Therefore, it would be advantageous to test for virulence of microbial partners of wood-inhabiting insects, as these are known to be of high risk for introduction (USDA 1994) Such information would be valuable in prioritizing both regulatory responses to avoid introduction by identifying the insect-microbe partnerships that are most likely to have substantive negative impacts on native trees.

Other needed research involving exotic forest insects and symbionts involves investigations into the degree of flexibility and fidelity that occurs among partners. Some mutualisms are relatively flexible, with partner shifts occurring commonly, albeit usually among taxonomically related groups. In the case of exotic insects, the acquisition of new symbionts may alter the range of tree hosts that can be used by the host or its ability to colonize particular substrates. Additionally, symbionts of exotic insects may be acquired by native insects which may result in exposure of a greater range of native trees to these symbionts, some of which may be phytopathogens.

Direct human impacts on forest structure and compositions

The direct effects of humans on forested landscapes will continue to affect critical mutualisms. The human population on Earth continues to increase and with this increase comes increased demands on ecosystems for space and resources. Fragmentation and conversion forest to agricultural lands continues at a rapid pace, particularly in developing countries. However, even in areas where the rate of deforestation is significantly less or where forests are actually increasing in extent, selective cutting, conversion from one forest type to another, alteration of genetic structure due to replanting with off-site seeds or seedlings, and fire suppression, continue to alter forests, their function and resilience, and organismal diversity. Unlike climate change, an understanding of the effects of various anthropogenic effects can be used to develop strategic approaches and policies to alleviate or reverse many of these negative impacts. However, with ever increasing demands on forests the ability to implement such measures will become increasingly difficult. An understanding of how various human activities affect individual organisms and their interactions with others (particularly mutualisms) will be key to developing the best, most effective measures to maintain functional, resilient forest and savanna ecosystems.

Conclusions

Forests and savannas have been heavily impacted by human activities including deforestation, fragmentation, loss of biodiversity, anthropogenic climate change, introduction of exotics, and alterations in forest composition, structure and disturbance regimes. Concern over these effects has given rise to a large number of studies focusing on impacts on individual species or on biotic community structure and composition. Much less common have been studies of impacts on critical interactions, especially mutualisms. Mutualisms, in general, have been seriously understudied until recent years (Janson *et al*. 2009). However, in the last two decades, studies on these interactions have virtually exploded in number, resulting in a new appreciation for their importance as major drivers of ecosystem process and function (Bronstein 1994).

Most organisms are involved in at least one mutualism, and many in several. Mutualisms facilitate the ability of partners to exploit otherwise marginal or inaccessible habitats and resources, and determine the ecological boundaries of many organisms (Janson *et al*. 2009). When perturbation or change disrupts, enhances or introduces new organisms into a mutualism, the outcome and stability of the original partnership(s) are altered as are the effects of the symbiosis on the community and ecosystem as a whole (Six 2009). This potential for human-induced environmental change to alter or decouple mutualisms is an area of critical need for research in ecology and evolution (Kiers *et al*. 2010).

In this paper, using examples from microbial-insect mutualisms in forest and savanna settings, we have tried to showcase how varied and complex the responses of mutualisms can be to an equally varied set of anthropogenic influences. In the process, we hope to have convincingly argued for the need to focus on community interactions, particularly mutualisms, when investigating the effects of anthropogenic change on natural systems. Researchers must be cognizant that many alterations in behaviors and distributions of organisms that are observed to occur in response to anthropogenic activities are likely being mediated by mutualists and other symbionts. Therefore, whether the goal is to understand the basic ecology of an organism, its response to anthropogenic or other types of environmental change, or to manage it as a pest, we argue that it is necessary to consider effects on hosts and symbionts in tandem. Additionally, it is clear that few mutualisms are being affecting by only a single anthropogenic factor, but rather most are being affected by multiple, often interacting, factors, adding an additional level of complexity that must be addressed.

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