PREDICTING FOREST INSECT DISTURBANCE UNDER CLIMATE CHANGE

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ABSTRACT

This paper comprises a review of literature regarding climate change impacts to forest insect disturbances. Its primary objectives were three-fold. First, commonalities were sought among systems regarding the effects associated with altered temperature and/or precipitation patterns on forest insect herbivores, the proximate and ultimate form of the response by the insects, and the outcome in terms of forest disturbance. Second, a general framework within which to assess future disturbances to temperate and boreal forests by insect herbivores was constructed. Finally, uncertainty regarding predictions of the extent/severity of forest insect disturbances under climate change into the future was discussed.

INTRODUCTION

There is now ample evidence that recent climatic changes have affected a broad range of organisms in a manner consistent with expectations from a warming environment (reviewed by Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Hickling et al. 2006, Post et al. 2009, Robinet and Roques 2010, Wolken et al. 2011). In fact, evidence has accumulated indicating direct effects of anthropogenic climate change on every continent, in every ocean and in most major taxonomic groups (Parmesan 2006). Among the major taxonomic groups in which impacts of global warming have been most frequently documented are the insects. Terrestrial insects are sensitive indicators of changes to the condition of abiotic and biotic systems (McGeoch 1998). Thus, the recent accumulation of evidence for climate change impacts to insect populations may be considered early symptoms of broad-scale, climate-induced ecological change.

Herbivorous insects are highly sensitive to variations in climate (Bale et al. 2002). Due to their short life cycles, reproductive potential, high mobility and physiological sensitivity to temperature, even modest changes in environmental conditions will result in rapid changes to their abundance and distribution. Climate change is expected to affect herbivorous insects through direct impacts to their development and survival, and/or indirect impacts mediated through trophic interactions and interactions with abiotic components of the environment (Ayres and Lombardero 2000, Hughes 2000, Harrington et al. 2001, Logan et al. 2003, Wolf et al. 2008). To date, direct and indirect impacts of changing climate to herbivorous insects have manifested as: increases (e.g. Logan and Powell 2001, Carroll et al. 2004) or decreases (Wilson et al. 2005) in thermally benign habitats; enhanced (Tenow et al. 1999, Logan and Powell 2001) or degraded (Visser and Holleman 2001, Musolin 2007) phenological synchrony among trophic levels and/or the environment; and reduced mortality from natural enemies (Stireman et al. 2005). Documented outcomes of these impacts to herbivorous insects are varied and include distributional, behavioral and ecophysiological changes. Distributional changes have become evident primarily as range expansions (e.g. Parmesan et al. 1999, Hickling et al. 2005, Musolin 2007), but also as range contraction (Wilson et al. 2005). Range changes have resulted in altered species interactions such as novel host-plant associations (Thomas et al. 2001, Braschler and Hill 2007, Cullingham et al. 2011), and escape from natural enemies (Menéndez et al. 2008). Behavioral changes have been recognized mainly among Lepidoptera with several species displaying altered patterns of habitat use (Thomas et al. 2001, Davies et al. 2006), and increased levels of migration (Sparks et al. 2007). Examples of ecophysiological responses to climate change by herbivorous insects are less common. However, Thomas et al. (2001) found an increased incidence of dispersive phenotypes by bush crickets (Orthoptera) in warming habitats, and similar responses have been quantified among non-herbivorous insects (Harada et al. 2005).

Although warming will not necessarily have positive implications for the fitness of all insect species (Chown and Terblanche 2006), there is evidence from historical global warming events that insect herbivory will generally increase (Wilf and Labandeira 1999). Indeed, Currano et al. (2008) found that the amount and diversity of insect damage to angiosperm leaves increased dramatically during an abrupt global warming event comparable in rate and magnitude to modern anthropogenic climate change (the Paleocene-Eocene Thermal Maximum, 55.8 million years ago). Based on this evidence, the authors concluded that elevated herbivory is likely to be a net long-term result of anthropogenic CO_2 emissions and resultant warming temperatures.

Herbivorous insects are common, ubiquitous elements of most terrestrial ecosystems. As a result of a long history of macroevolutionary interactions, most herbivorous insects live in benign or even beneficial relationships with their host plants (Farrell et al. 1992). In fact, evidence suggests that herbivorous insects are integral to biomass decomposition, carbon and nutrient cycling, and energy flow (Haack and Byler 1993), and may ultimately function as regulators of primary productivity (Mattson and Addy 1975). Although the vast majority of insect herbivores are relatively innocuous, a small number of species are capable of explosive population eruptions that frequently have considerable economic and ecological ramifications. Amongst the most apparent of these eruptive species are those that occur in temperate and boreal forests where outbreaks periodically cause growth loss and mortality of trees over large landscapes.

Despite the long-lived nature of temperate and boreal forests, when considered over broad spatial scales they are highly dynamic systems prone to abrupt episodes of change via natural disturbance. Natural disturbance is an integral component of these forests and is necessary to the maintenance of their biodiversity and ecosystem stability (Pickett et al. 1987). It is also a fundamental component of carbon dynamics. Forest ecosystems comprise major reservoirs of carbon. The net contribution that forests make to the global atmospheric carbon balance derives from the difference between uptake of CO_2 by photosynthesis, release of CO_2 by autotrophic and heterotrophic respiration, and release of CO_2 (and CH_4, N_2O) by disturbance (e.g. Kurz and Apps 1999). Changes in one or more of these fluxes can cause forests to act either as a net sink or source of greenhouse gases. It is generally accepted that during the latter half of the previous century northern and temperate forests comprised a large carbon sink (Fan et al. 1998, Goodale et al. 2002, but see Stephens et al. 2007). More recently, however, these terrestrial carbon sinks have weakened (Fung et al. 2005, Canadell et al. 2007, Piao et al. 2008). Evidence suggests that an increase in natural disturbance may have played a large role in the decrease in forest ecosystem carbon storage (Kurz and Apps 1999), and could overwhelm efforts to mitigate climate change through forest management activities (Kurz et al. 2008b).

Forest insects comprise one of the largest sources of natural disturbance in temperate and boreal forests (e.g. Nilsson et al. 2000 and references therein, Dale et al. 2001, Schelhaas et al. 2003). This is especially true in North American forests where insect herbivory is the largest absolute source of natural disturbance (e.g. Dale et al. 2001, Raffa et al. 2008). Given the sensitivity of herbivorous insects to variations in climate (e.g. Bale et al. 2002), combined with evidence of historical increases in herbivory associated with a warming environment (Currano et al. 2008), climate change is expected to have a significant impact on the dynamics of forest insect herbivores and the extent/severity of their disturbances in northern forests. An increase in insect-caused forest disturbance beyond the long-term range of natural variability could significantly reduce forest carbon reservoirs, increase rates of heterotrophic respiration and cause feedback to future climate change (Kurz et al. 1995, 2008a, but see O'Halloran et al. 2011).

The primary objectives of this paper are three-fold. First, the accumulating evidence for direct climate-induced changes to natural disturbance in forests by insect herbivores will be reviewed. Specifically, the review will seek commonalities among systems in the effects associated with altered temperature and/or precipitation patterns on forest insect herbivores, the proximate (i.e. individual) and ultimate (i.e. population) form of the response by the insects, and the outcome in terms of forest disturbance. Second, based upon this review, a general framework within which to assess future disturbances to temperate and boreal forests by insect

herbivores will be proposed. Finally, uncertainty regarding predictions of the extent/severity of forest insect disturbances under climate change into the future will be discussed.

METHODS

As a result of the widespread expectation that disturbances caused by forest insects will increase due to global warming, there has been a plethora of recent studies that mathematically model the dynamics of populations in a warming environment (Williams 1995, Logan and Powell 2001, Régnière et al. 2009, Seidl et al. 2009, Bentz et al. 2010, Régnière et al. 2010, Evangelista et al. 2011, Jönsson et al. 2011, Sambaraju et al. 2012, Kausrud et al. 2012, Coops et al. 2012). Similarly, many recent investigations have claimed direct empirical links between climate change and altered insect dynamics, although frequently the link is only tenuous (Logan et al. 2003, Parmesan and Yohe 2003, Hickling et al. 2006). This review considers only those studies which directly attribute the effects of anthropogenic climate change to altered disturbance patterns by forest insects. Direct measures of climate change impacts on the dynamics and impacts of forest insect populations are often temporally intractable (Logan et al. 2003); therefore correlations and/or "space-for-time' substitutions are often utilized as surrogates for longer-term investigations. To ensure that the studies considered in this analysis engender as little equivocation as possible regarding links to climate change, each must involve quantification of at least two of the following three aspects associated with an eruptive forest insect:

    i)   a causal link between an aspect of climate/weather and a critical life history parameter affecting individuals and/or populations;

    ii)   a documented change in population dynamics associated with a change in climatic conditions beyond the long-term natural range of variability, and;

    iii)   a documented change in the frequency, extent and/or severity of disturbance associated with a change in climatic conditions beyond the long-term natural range of variability

To facilitate identification of patterns among diverse systems, studies meeting the above criteria were evaluated and a series of standardized parameters were extracted and collated (see Table 1). Insect disturbance agents were assigned to their appropriate feeding guild; here defined as a group of species that exploit the same class of resources in a similar way (Root 1967). Then, the region in which the study was conducted was recorded, and climatic changes (temperature and precipitation) within each region during the past several decades were extracted from the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report (IPCC 2007a, 2007b). Although mean decadal changes in temperature and precipitation across regions may be too coarse to reflect the climatic phenomena that influence insect populations (Logan et al. 2003), the highly specific nature of the change(s) in climate at the center of each investigation, such as degree-day accumulation or the occurrence of extreme winter minima, preclude collation of a list of standardized metrics across studies. Instead, to capture fine-scale drivers of change, the climate-induced alterations to ecological processes that affected the insect herbivore, hereafter termed "ecological forcings", were identified. The impact of the ecological forcing on individuals (proximate) and populations (ultimate) of the forest insect were determined where possible. Finally, the outcome of the climate-change altered insect dynamics on forest disturbance (positive or negative) were determined. In cases where only two of the three initial criteria outlined above were satisfied, related studies (where available) that provided quantification of the third criterion were also considered.

RESULTS AND DISCUSSION

General considerations

Despite the apparent consensus that climate warming will have significant impacts on insect populations, only 17 studies representing 11 forest insect species presented unequivocal evidence of climate change impacts to their disturbance patterns (Table 1). Links between aspects of climate/weather and critical life history parameters have been established for a great many forest insects (e.g. Wallner 1987); however, documented changes in population dynamics and resultant impacts to forests associated with a change in climatic conditions beyond the long-term natural range of variability are rare. This may be due to the very recent manifestation of changes in climate sufficient to affect ecosystem processes and/or the lack of relevant climate data at an appropriate spatial scale at which conduct assessments.

Of the 11 insect disturbance agents considered, three belong to the bark beetle guild and eight to the defoliator guild (Table 1). Bark beetles are a group of insects (order Coleoptera) that feed within the phloem of their host trees. Species in this guild that are significant eruptive disturbance agents generally must kill their host to successfully reproduce. By contrast, defoliators feed freely on the leaves of their host trees, and generally only cause tree mortality after multiple seasons of severe impacts. All of the eight defoliators identified in this investigation belong to the order Lepidoptera. It is unsurprising that all of the examples identified are limited to two taxonomic groups since the vast majority of forest insect disturbance agents are in the orders Coleoptera and Lepidoptera (Nothnagle and Schultz 1987).

Regions experiencing climate change-altered forest insect disturbances were largely confined to the northern hemisphere; only a single documented case originated in the southern hemisphere. Three examples occurred in western North America, six in Europe and Scandinavia, and one in South America (Table 1). This result was expected given that the majority of forests occur north of the equator (FAO 2001). Despite the coarse estimate of climatic changes at the regional scale, all studies were associated with significant increases in mean annual temperature during the past several decades (Table 1). This result is noteworthy since warming is not uniform, and some regions had not experienced significant changes during the period considered by this review (IPCC 2007b). In contrast to temperature, there was no apparent trend in changes in precipitation; some regions experienced increases, others decreases, and still others exhibited no detectable changes (Table 1). The relationship between precipitation and the dynamics of forest insect disturbance agents is complex, and increases or decreases do not systematically result in higher or lower disturbance rates (Raffa et al. 2008, Jactel et al. 2012).

Altered ecological interactions affecting insect disturbances resulting from climate change (i.e. ecological forcings) were extremely diverse (Table 1). Warmer temperatures were relevant both during periods of insect activity (i.e. summer) and dormancy (i.e. winter and spring). Moisture deficits at particular times of the year were often important, especially for the bark beetles. By contrast, phenological matches and mismatches due to increased heat accumulation were particularly important for defoliators. The most common proximate response by insects to ecological forcing was increased or decreased survival of juvenile life stages (Table 1). For the bark beetles, an increase in the colonization success by adults was also common. Shorter generation times (i.e. reduced voltinism) were documented for individual species within the bark beetle and defoliator guilds. The ultimate response by insect populations to ecological forcing also tended to be rather variable, but in all cases significant changes in dynamics were

observed (Table 1). Range expansion was common amongst both bark beetles and defoliators. All of the bark beetle species responded to climate change by increasing their outbreak severity. For defoliator populations, responses to a warming environment were more complex. In equal numbers of cases, defoliator species exhibited increased and decreased outbreak severity/frequency. The outcomes in terms of forest disturbance were directly related to the response by the insect populations (Table 1).

Emerging patterns
　　　　Although the response by insect disturbance agents to climate change was varied, patterns within feeding guilds are apparent. These patterns can be discerned in terms of both the ecological forcing associated with a warmer environment and the proximate and ultimate response on the part of the forest insect.

Bark beetles: In western North American forests, bark beetles are the most ecologically and economically important insect herbivores. Since 2000, they have collectively caused the mortality of nearly 47 million hectares of trees from Mexico to Alaska (Raffa et al. 2008). Although outbreaks in recent years have potentially been aggravated by forest management activities (Taylor and Carroll 2004, Aukema et al. 2006), climate change has clearly intensified their extent and severity (Table 1). The capacity for some bark beetle species to spread rapidly over large landscapes derives from a common eruptive dynamic that is characterized by a threshold separating domains of negative (endemic) and positive (epidemic) feedbacks (Safranyik and Carroll 2006, Raffa et al. 2008). In the endemic domain, negative feedbacks arise from limited host availability/suitability, competition and the action of natural enemies, whereas in the epidemic domain positive feedbacks manifest when higher beetle numbers facilitate attacks on vigorous, nutritionally optimal trees (Raffa et al. 2008, Boone et al. 2011). Weather is the most common density independent perturbation to the trophic interactions that constrain beetles to the endemic domain, and even relatively short-lived changes may reduce generation mortality sufficiently for populations to breach the endemic-epidemic threshold and amplify across spatial scales (Safranyik and Carroll 2006, Aukema et al. 2008, Raffa et al. 2008).
　　　　Arguably the most spectacular example of climate-change exacerbated disturbance by a forest insect can be seen in the massive outbreak by the mountain pine beetle in the pine forests of western North America. Carroll et al. (2004) used an empirical model of climatic suitability together with historic climate data and infestation maps to show that as a result of a warming environment mountain pine beetles had rapidly expanded their range into higher elevations and latitudes during the latter portion of the 20th century. At the same time, warmer conditions improved overwintering survival of juvenile beetles, and spring drought facilitated subsequent colonization success of host trees by adults (see Table 1). The sensitivity and rapid response by mountain pine beetle to climate spawned a series of studies predicting its continued range expansion and potential colonization of high elevation pine ecosystems, and the pine forests of the entire North American boreal region (Logan and Powell 2001, Safranyik et al. 2010, Logan et al. 2010, Bentz et al. 2010, Sambaraju et al. 2012, Coops et al. 2012). In keeping with these predictions, the mountain pine beetle outbreak has spread across approximately 16 million hectares, breached the Rocky Mountain geoclimatic barrier (Safranyik and Carroll 2006, de la Giroday et al. 2011, 2012) and has recently entered the western portion of the boreal forest in Canada (Safranyik et al. 2010, Cullingham et al. 2011).

The spruce beetle outbreak, which spread over vast areas of northwestern North America during the 1990s, has been linked to a complex interaction of the direct effects of warming on the beetle, and indirect effects on host-tree susceptibility (Table 1) (Sherriff et al. 2011). Evidence suggests that heat accumulation associated with unusually warm summers caused a shift in voltinism from the predominant two-year cycle to a one-year cycle, thereby doubling the rate of increase and spread of populations (Hansen and Bentz 2003, Berg et al. 2006). The combination of warmer temperatures and drought stress also reduced host-tree vigour and putatively increased tree susceptibility and colonization success by adult beetles across extensive areas (Barber et al. 2000, Berg et al. 2006, Sherriff et al. 2011).

The pinyon ips beetle, a previously unknown disturbance agent, underwent an extensive eruption in the pinyon pine–juniper woodlands of southwestern North America following a drought accompanied by high temperatures during 2002 and 2003 (Breshears et al. 2005, 2009, Santos and Whitham 2010). Although such droughts are not unprecedented and therefore are not necessarily associated with climate change, the abnormally high temperatures that exacerbated host stress are likely a product of ongoing warming due to anthropogenic greenhouse gas emissions (Table 1) (Breshears et al. 2005). Diminished tree vigour as a consequence of drought stress increased tree susceptibility and the colonization success of adult pinyon ips beetles (Santos and Whitham 2010).

Reduced host-tree vigour as a consequence of drought stress is common to each of the examples of climate-change aggravated bark beetle outbreaks (see Table 1). It has been suggested that tree stress arising from unusual weather patterns may be the primary factor underlying broad-scale biotic disturbances in forest ecosystems throughout the world (White 1984, Mattson and Haack 1987, Ayres and Lombardero 2000). Although the generality of this assertion has been questioned (Larsson 1989), it is accepted that bark beetles are particularly responsive to stress in their host trees since a tree's capacity to defend itself against attack is directly related to its vigour (Christiansen and Waring 1987, Herms and Mattson 1992). As long as forests are subject to increasing stress as a result of global climate change, it is very likely that disturbances from bark beetles will increase in frequency, extent and severity.

Defoliators: Many lepidopteran defoliators exhibit highly regular cycles in abundance as a consequence of delayed density-dependent processes such as depredations by predators and/or parasitoids (Berryman 1996). Fluctuations about these cycles typically result from perturbations exerted by extrinsic density-independent factors (Royama 1992). Generally, drought does not exacerbate defoliator outbreaks since these insects tend not to respond positively to stress in their host trees (Larsson 1989). Support for this assertion can be found in the present review where in no instance was drought implicated as an ecological forcing in defoliator dynamics (see Table 1).

Simple density-independent perturbations were apparent among several defoliators exhibiting climate-induced increases in disturbance. Warmer winters have resulted in higher survival rates for the pine processionary moth (Battisti et al. 2005), the winter moth and the autumnal moth (Jepsen et al. 2008). For the pine processionary moth, warmer winters have facilitated feeding and survival by larvae. During the past several decades, ameliorating temperatures have enabled processionary moth populations to expand to higher elevations and latitudes (Battisti et al. 2005, 2006). Similarly, the winter moth and autumnal moth have expanded their outbreak ranges in recent years within Fennoscandia as a consequence of ameliorating temperatures and increased survival of overwintering life stages (Hagen et al. 2007, Jepsen et al. 2008). A density-independent exacerbation of defoliator dynamics and impacts was

also detected in the only example from the southern hemisphere. *Ormiscodes amphimone* is an eruptive lepidopteran defoliator of the beech forests of the southern Andes Mountains. Warmer and drier conditions during the past several decades are associated with an increase in the frequency of outbreaks (Paritsis and Veblen 2011). The altered dynamics of *O. amphimone* have been attributed to a temperature-driven increase in the rate of foliage consumption by larvae and an associated increase in their developmental rates (Paritsis and Veblen 2010).

For many leaf-feeding herbivores, synchrony in phenology with their host plant is critical to their fitness since development outside a narrow phenological time window has severe negative consequences (reviewed by Van Asch and Visser 2007). Accordingly, the most common form of ecological forcing affecting defoliator populations and their disturbances within forests found in this study was altered phenological synchrony (Table 1). Indeed, climate change-driven alterations to the synchrony between the flush of highly nutritious new foliage and the emergence of defoliator feeding stages were found to significantly affect the dynamics of five of the eight defoliator species considered in this review (see Table 1). Interestingly, the impact of altered phenological synchrony to the dynamics and disturbance rates of defoliators was both positive and negative. As a consequence of a warming environment, two formerly innocuous defoliators, the scarce umber moth (Jepsen et al. 2011) and the birch bud moth (Tenow et al. 1999), have experienced improved synchrony between egg hatch and bud burst of their primary host, mountain birch in Fennoscandia. As a result, the scarce umber moth has rapidly expanded its northward range (Jepsen et al. 2011), while birch bud moth populations reached unprecedented epidemic densities (Tenow et al. 1999). By contrast, the larch bud moth in the Alps (Johnson et al. 2010) and the winter moth in the Netherlands (Visser and Holleman 2001) have experienced phenological mismatches between bud burst of their host trees and emergence of their larvae due to climate change. In the case of the larch bud moth, this phenological asynchrony has brought to an end 1200 years of consistent, regular population cycles (Esper et al. 2007, Büntgen et al. 2009, Johnson et al. 2010). For the winter moth, climate change has caused asynchrony in the southern portions of its range, and effected a decline in populations there (Visser and Holleman 2001), but as mentioned above this has been offset by improved overwintering survival in the northern portion of its range (Jepsen et al. 2008). Therefore, it is likely that with additional warming winter moth populations will continue to expand northward in Scandinavia, while contracting in Europe.

The final example of the negative aspects of phenological mismatching due to climate change comprises the pine moth in South Korea. In this case asynchrony is an indirect consequence of altered voltinism. An increase in mean annual temperature has caused pine moth populations to switch from one generation per year (univoltine) to two generations per year (bivoltine). Offspring of the second generation emerging later in summer do so long after bud burst of their host trees, and therefore suffer high levels of mortality (Choi et al. 2011). Consequently, outbreak extent and severity has declined.

The variable responses by defoliating insects to climate change precludes simple predictions regarding future forest disturbances by this feeding guild under climate change. Whereas fitness benefits may result from reduced mortality or improved phenological synchrony in a warmer environment, they may be offset by increased mortality due to altered development rates and/or phenological mismatching. Additional research is required to develop reliable, generalizable predictions of defoliator responses to climate change that incorporates all relevant trophic interactions.

A predictive framework

Although detailed predictions of the specific response by a given insect disturbance agent may be not be possible at this time, generalizations can be made with respect to the type of response that broad groups of disturbance agents will exhibit irrespective of their feeding guild. Potential insect disturbance agents may exhibit landscape-level responses to climate change in one the following four categories, depending on their spatial and temporal ubiquity. For species that can be found throughout their host-tree distribution (i.e., native ubiquitous species), a warming environment has the potential to affect the frequency, duration, and severity of disturbance events. For species that are native but do not occupy the entire distribution of their host trees (i.e., native invasive species), climate change will potentially affect the range over which disturbances will occur, as well as the frequency, duration, and severity of disturbance events. For species that are native but have historically not caused notable impacts (i.e., native innocuous species), changing climate has the potential to alter population dynamics and allow widespread disturbance. Finally, for introduced species (i.e., alien invasive species), a warming environment may increase the probability that the species will establish itself, persist, and have a greater impact in the future. It should be stressed that these generalizations do not preclude other possible impacts of climate change on biotic disturbance agents in each of the categories. For example, (Volney and Fleming 2000) proposed that climate change may facilitate host switching by some herbivorous insects, which in turn may result in (additional) range expansion by organisms.

The utility of the predictive framework described above can be illustrated by applying it to the cases presented in Table 1. The spruce beetle, larch budmoth, pine moth and *O. amphimone* are native ubiquitous species. Climate change has affected, negatively or positively, the frequency, duration, and severity of associated disturbance events. The mountain pine beetle, pine processionary moth, winter moth and autumnal moth can be considered native invasive species. A warming environment has caused an expansion in the range over which disturbances have occurred, and to a lesser degree affected the severity of those disturbances. The pinyon ips beetle, scarce umber moth and birch bud moth are native innocuous insects that have not historically caused large forest disturbances. However, changing climate has altered their population dynamics and allow widespread impacts. Finally, although no examples of alien invasive species were considered in this review, there are many that are projected to establish, persist, and have a greater impacts in the future. Perhaps the gypsy moth in Canada is the best example (Régnière et al. 2009). For any potentially eruptive insect species, given basic information on its spatial distribution and pervasiveness, the suite of potential responses to a warming environment can be defined.

Considering uncertainty

Uncertainty regarding forecasts of the impacts of forest insect disturbances under climate change is highly nonlinear. Indeed, in the near to medium term (i.e., up to 2070), uncertainty may actually decrease. This is due to the tendency for tree species that have established on a site to persist there long after the conditions that led to their establishment have disappeared (Payette 1993). As a result, in the face of a rapidly changing climate, the current structure of forests (in terms of distribution and species composition) will change relatively slowly, and therefore forests will be prone to widespread climate-induced stress. As discussed above, it is widely considered that tree stress arising from unusual weather patterns, such as those anticipated with climate change, may be the primary factor underlying broad-scale biotic disturbances in forest

ecosystems throughout the world, particularly from bark beetles (reviewed by Raffa et al. 2008). Thus, as long as existing forests are subject to increasing stress as a result of global climate change, it is very likely that they will experience elevated levels of disturbance. Although disturbance is normal in most ecosystems and not inherently detrimental, impacts that are outside the range of natural variability can result in ecosystem degradation that is self-reinforcing and irreversible (Folke et al. 2004). In the longer term (i.e., up to 2100), given additional climate change and elevated disturbances that fall beyond the range of natural variability, forests and the suite of disturbance agents operating in them are unlikely to resemble those with which we are currently familiar. Therefore, the level of uncertainty regarding forest insect disturbance will increase dramatically to the point that it will become impossible to predict the magnitude of their impacts

Conclusions

The preceding analysis suggests that disturbance by bark beetles is more likely to be exacerbated by climate change than defoliators, mainly because of the former's positive response to host tree stress and lack of a requirement for strict phenological synchrony. Given that there is little doubt of climate change-aggravated disturbance by bark beetle populations occurring already, priority should be given to development of realistic predictive tools that will facilitate proactive strategies intended to minimize impacts. Vigilance toward native innocuous, native invasive and alien invasive species should also be stressed due to their potential to erupt unpredictably in space and time. For example, lesser known bark beetle species occurring in the southern regions of North America have the potential to move northward as temperatures increase (Gan 2004, Bentz et al. 2010). Although the response by defoliators may be less predictable compared to bark beetles, their potential to cause disturbances over vast areas of forest cannot be ignored. The predictive framework suggested in this study provides a suite of potential outcomes for an eruptive forest defoliator under climate change; however, research efforts should focus on the development of predictive models of defoliator dynamics in a warming environment.

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Table 1. Documented impacts of climate change on forest insect disturbance agents

Disturbance agent	Feeding guild[1]	Region	Mean regional changes		Ecological forcing[4]	Insect response		Disturbance outcome	Reference
			Temp.[2] (°C)	Precip.[3] (%)		Individual (proximate)	Population (ultimate)		
Mountain pine beetle (*Dendroctonus ponderosae*)	Bark beetle	Northwestern North America	1.0 – 2.0	No change	Elevated growing season temperatures; warmer winter minima; spring drought	Increased larval survival; higher colonization success	Increased outbreak severity; range expansion	+	Carroll et al. 2004
Spruce beetle (*D. rufipennis*)	Bark beetle	Alaska	1.0 – 2.0	3 – 15	Elevated growing season temperatures; late summer drought	Shorter generation time; higher colonization success	Spatial outbreak synchrony; increased severity	+	Sherriff et al. 2011
Pinyon ips beetle (*Ips confusus*)	Bark beetle	Southwestern North America	1.0 – 2.0	-3 – -15	Multiannual temperature-exacerbated drought	Increased colonization success	Landscape-scale outbreak; increased severity	+	Breshears et al. 2005, 2009; Santos & Whitham 2010
Pine processionary moth (*Thaumetopoea pityocampa*)	Defoliator	Northern Italy (Alps)	0.2 – 1.0	-3 – -15	Warmer mean winter temperatures	Increased larval survival	Range expansion	+	Battisti et al. 2005, 2006
Larch budmoth (*Zeiraphera diniana*)	Defoliator	European Alps	0.2 – 1.0	-3 – -15	Warmer winters; advanced bud burst; degraded phenological synchrony	Reduced egg and larval survival	Reduced outbreak periodicity	-	Esper et al. 2007; Buntgen et al. 2009; Johnson et el. 2010
Winter moth (*Operophtera brumata*)	Defoliator	Netherlands/ Fennoscandia	1.0 – 2.0/ 0.2 – 1.0	No change / 3 – 15	Warmer springs; altered phenological synchrony	Reduced/ increased larval survival	Range contraction/ expansion	-/+	Visser & Holleman 2001/ Jepsen et al. 2008
Autumnal moth (*Epirrita*	Defoliator	Fennoscandia	0.2 – 1.0	3 – 15	Warmer mean annual and winter	Increased egg	Range	+	Jepsen et al.

Disturbance agent	Feeding guild[1]	Region	Mean regional changes		Ecological forcing[4]	Insect response		Disturbance outcome	Reference
			Temp.[2] (^{o}C)	Precip.[3] (%)		Individual (proximate)	Population (ultimate)		
Scarce umber moth (*Agriopis aurantiaria*)	Defoliator	Fennoscandia	0.2 – 1.0	3 – 15	Warmer springs; advanced egg hatch; improved phenological synchrony	Increased larval survival	Range expansion	+	Jepsen et al. 2011
Birch bud moth (*Argyresthia retinella*)	Defoliator	Fennoscandia	0.2 – 1.0	3 – 15	Warmer mean annual temperatures; improved phenological synchrony	Increased overwintering survival	Landscape-scale outbreak; increased severity	+	Tenow et al. 1999
Pine moth (*Dendrolimus spectabilis*)	Defoliator	South Korea	1.0 – 2.0	3 – 15	Warmer mean annual temperatures; degraded phenological synchrony (2nd generation)	Shorter generation time; reduced larval survival	Reduced outbreak extent/severity	-	Choi et al. 2011
Ormiscodes amphimone	Defoliator	Patagonia	0.2 – 1.0	No change	Warmer and drier springs	Increased consumption and growth rates	Increased outbreak frequency	+	Paritsis & Veblen 2010, 2011

[1]As defined by Root (1967)
[2]From 1970 to 2004 (IPCC 2007a)
[3]Change per decade from 1979 to 2005 (IPCC 2007b)
[4]Defined as the climate change-induced alteration to ecological interactions affecting the insect herbivore.