Universitat Autònoma de Barcelona

Incorporating insect pest outbreaks to landscape modelling: the case of Cydalima perspectalis invasion in Europe

QUIM CANELLES TRABAL

Incorporating insect pest outbreaks to landscape modelling: the case of *Cydalima perspectalis* invasion in Europe

---

QUIM CANELLES TRABAL

Il·lustració de portada: Gerard Nel·lo Tubau | Disseny i maquetació: Alba Font Villar

Incorporating insect pest outbreaks to landscape modelling: the case of *Cydalima perspectalis* invasion in Europe

DISSERTATION PRESENTED BY QUIM CANELLES TRABAL
TO OBTAIN THE DEGREE OF DOCTOR.

Supervised by	**Tutored by**
Lluís Brotons Alabau	**Javier Retana Alumbreros**
CSIC-CREAF	**CREAF**

Doctoral program of Terrestrial Ecology
Centre de Recerca Ecològica i Aplicacions Forestals
Universitat Autònoma de Barcelona

Barcelona, June 2021

**“La Natura ens murmura,
però només a mitges, el secret.”**

MARIÀ MANENT,
PLOTÍ VA DIR, 1986

→ Agraïments

El valor d'una tesi doctoral, al meu entendre, és l'aprenentatge que experimenta un aspirant a doctor. Es tracta d'un aprenentatge principalment acadèmic, però també personal, emocional, social i professional. En el meu cas, aquest creixement s'explica gràcies a les relacions precioses establertes amb gent excepcional. És un gust poder mencionar aquí la seva aportació en aquest treball, però sobretot agrair tot el que ells i elles han significat per a mi en aquest bonic procés.

Primer de tot vull agrair al Lluís Brotons l'oportunitat de fer aquesta tesi i la confiança mostrada des del primer moment. Treballar amb ell ha estat aprendre constantment: aprendre a apassionar-me pel que faig, a aprofitar i crear oportunitats, a prendre decisions i a pensar sempre una mica més enllà. Fins i tot he après a aplicar tot això a les partides d'escacs que compartim.

Durant aquests tres anys, he tingut la sort de tenir uns referents de qui aprendre i amb qui anar creixent dia a dia: la Núria Aquilué, l'Andrea Duane i l'Aitor Ameztegui. Ells, cadascú a la seva manera, m'han cuidat incondicionalment tant si els ho demanava com si no, m'han fet de mentors tan professional com personalment i, el que més feliç em fa, m'han fet sentir afortunat al compartir la seva amistat. Tot és més fàcil amb aquests germans grans!

En aquesta tesi hi ha bocins de moltes persones que han sumat significativament, ja sigui aportant una idea, una opinió o simplement una paraula. Aportacions que surten gràcies a converses desinteressades, passejades pel bosc, col·laboracions estretes i d'altres de més llunyanes, acolliments, amistats, entusiasmes, etc. Gràcies per aquests bocins a l'Emili Bassols, Jordi Vayreda, Patrick James, Josh Lawler, Pere Navarro, David Shaw, Garret Meigs, Meg Krawchuk, Gabriela Ritokova, Rick Kelsey, Henrly Lee, Keith Reynolds, Núria Roura, Jonàs Oliva i Alba Font.

I agraeixo també tot el creixement personal que no es podria entendre sense la gent del CTFC i les aventures que ens hem inventat a la remota Solsona.

Finalment, em dono el gust de dedicar aquesta tesi. La dedico al Gerard, amb qui vaig compartir tots els passos de la carrera de biòleg i amb qui encara voldré compartir els que vindran. La dedico als avis i a la seva manera d'estimar. I la dedico a la Berta i a totes les alegries que vol compartir amb mi.

→ TABLE OF CONTENTS

INTRODUCTION

CHAPTER 1:

GLOBAL REVIEW ON INTERACTIONS BETWEEN INSECT PESTS AND OTHER FOREST DISTURBANCES

CHAPTER 2:
PREDICTING THE POTENTIAL DISTRIBUTION AND IMPACT OF THE INVASIVE SPECIES *CYDALIMA PERSPECTALIS* IN EUROPE

CHAPTER 3:
ANTICIPATING *B. SEMPERVIRENS* VIABILITY IN FRONT OF *C. PERSPECTALIS* OUTBREAKS, FIRE, AND DROUGHT DISTURBANCES.

GENERAL DISCUSSION AND CONCLUSIONS

Preface

The present thesis is the result of the work carried out by Quim Canelles Trabal between 2018 and 2021. The thesis was developed in Centre de Ciència i Tecnologia Forestal de Catalunya (Solsona) and includes an internship in USFS Corvallis (Oregon, USA). From the work derived from this thesis, the following articles were published or are about to be published in international scientific journals:

Canelles, Q., Aquilué, N., James, P. M., Lawler, J., Brotons, L. 2021. Global review on interactions between insect pests and other forest disturbances. *Landscape Ecology*, 1-28. Doi: doi.org/10.1007/s10980-021-01209-7

Canelles, Q., Bassols, E., Vayreda, J., Brotons, L. 2021. Predicting the potential distribution and forest impact of the invasive species *Cydalima perspectalis* in Europe. *Ecology and Evolution*. Doi: doi.org/10.1002/ece3.7476

Canelles, Q., Aquilué, N., Brotons, L. Anticipating *B. sempervirens* viability in front of *C. perspectalis* outbreaks, fire, and drought disturbances. Under revision in *Science of Total Environment*.

Abstract

Insect pests are integrated elements of forest landscape dynamics. However, an increase in the number of pest outbreaks and in their impact has been experienced in recent decades, causing severe consequences for ecosystems and society. The reasons behind these changing dynamics are mainly related to changes in land-use, climate, and the introduction of invasive species due to international trades and human mobility. The central goals of this thesis are to advance in the understanding of insect pest impacts on forest landscapes and to integrate them in modelling tools that help the prediction of consequences in a global change future. To face these goals, I defined the direct and indirect effects of insect pests and their interactions with other forest landscape disturbances (fire, drought, storms, pollution, etc.), and described the mechanisms underlying these responses. Aiming at working on a specific actual concerning pest, I examined the case of boxwood moth (*Cydalima perspectalis*), a Lepidoptera native to Asia and invasive in Europe since 2007. I described the ecologic niche of the species as well as its distribution and potential impact on the invaded area. Finally, I anticipated impacts of this pest and its interactions with other disturbances in the Southern Pyrenees under future climatic conditions.

In this thesis, I proposed different methodologies to study the impact of forest pests. First, I demonstrated that a combination of information from the native and invaded areas is required for a correct application of Species Distribution Models (SDMs) in invasive species. Second, I evidenced that spatially explicit simulation models are appropriate tools for the study of forest disturbances, identifying key parameters in determining their dynamics, analyzing their interactions, and anticipating their impacts in the face of global change uncertainty. Finally, I highlighted the adequacy of differentiating the presence versus the severity of a disturbance in order to effectively apply the methodologies described.

The results presented in this thesis provide new evidence of the processes governing pest dynamics – and their associated impacts – on forest functioning, in particular, the case of *C. perspectalis*. I demonstrated that the distribution of *C. perspectalis* in the Southern Pyrenees depended on the presence of the host plant (*Buxus sempervirens*) and the insect spread capacity (which is usually altered by involuntary anthropochory), while it was not limited by the fragmentation or heterogeneity of the habitat. However, severe defoliation was only found in places with high climatic suitability, defined by low seasonal precipitation and temperature, and low temperature diurnal range. These conditions define a continentality pattern where the most endangered boxwoods were those located near the coast and at low elevation (in the provinces of Girona, Barcelona, and Navarra) and excluding areas of the central Pyrenees (Lleida, Huesca). Future projections of *C. perspectalis* impact describe a cyclic consumer-resource relationship with the host plant. In addition, climate change may reduce the area of severe impact being concentrated only in few locations. The interaction between *C. perspectalis* and extreme drought was not significant. However, as I reported for other forest pest species, interactions with other disturbances are complex and occur in various directions, effects (antagonistic and synergistic) and spatial and temporal scales. For instance, trees that are damaged by fire or drought can synthesize ethanol, monoterpenes, and pheromones that attract insects; trees killed by an insect pest result in an accumulation of fuel that facilitates the spread of fires; trees weakened by drought have a lower response capacity (resin synthesis, regrowth capacity, etc.) and are therefore more susceptible to insect attacks. All this information offers a valuable basis for future research and for designing forest and pest management actions.

Resum

Les plagues d'insectes són elements integrats a la dinàmica del paisatge forestal. Tot i això, durant les últimes dècades, han experimentat un augment en nombre i impacte, implicant conseqüències severes pels ecosistemes i la societat. Els motius d'aquesta dinàmica són principalment els canvis en l'ús del sòl, els canvis en el clima i la introducció d'espècies invasores degut al comerç internacional i a la mobilitat humana. L'objectiu central d'aquesta tesi és avançar en el coneixement de l'impacte de les plagues d'insectes al paisatge forestal i integrar-lo en eines de modelització que ajuden a la predicció de conseqüències en un futur canviant. Hem basat l'aproximació en definir els efectes directes i indirectes de les plagues d'insectes mitjançant la descripció de les interaccions amb altres pertorbacions del paisatge forestal (el foc, la sequera, les tempestes, la contaminació, etc.) i descriure els mecanismes que hi influeixen. Hem exemplificat el paper de les plagues forestals amb el cas d'estudi de la papallona del boix (*Cydalima perspectalis*), un lepidòpter originari d'Àsia i invasor a Europa des de 2007. Hem descrit el nínxol ecològic de l'espècie així com la seva distribució i impacte potencial a l'àrea d'invasió. Finalment hem anticipat els impactes d'aquesta plaga i les seves interaccions amb altres pertorbacions a la vessant sud dels Pirineus en un futur regit pel canvi climàtic.

Aquesta tesi proposa diferents metodologies per a l'estudi de les plagues forestals i el seu impacte al paisatge. Primer es demostra que per una correcta aplicació dels *Species Distribution Models* (SDM) en espècies invasores és necessària la combinació d'informació de la zona nativa i la zona d'invasió. Segon, s'ha evidenciat que els models de simulació espacialment explícits són eines adequades per descriure les pertorbacions forestals, identificar els paràmetres clau de la seva dinàmica, analitzar les seves interaccions i anticipar els seus impactes davant la incertesa del canvi global. Finalment, es constata que per tal de fer una aplicació eficaç de les metodologies descrites és necessari diferenciar l'ocurrència d'una pertorbació de la severitat del seu impacte.

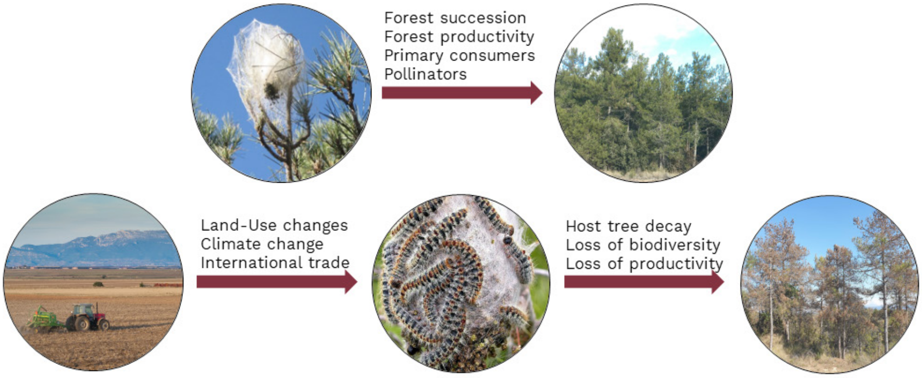
Els resultats aquí exposats proporcionen noves evidències dels processos que regeixen la dinàmica de plagues forestals i, en concret, de *C. perspectalis*. Es demostra que la distribució de *C. perspectalis* al sud dels Pirineus depèn de la presencia de la planta hoste (*Buxus sempervirens*) i la capacitat d'expansió de l'insecte (que es veu normalment alterada per introduccions antropocòries involuntàries), mentre que no és limitada per la composició de l'habitat. Tot i això, la defoliació severa només es troba en llocs d'alta adequació climàtica, definida per un rang de temperatures diürnes petit i una baixa estacionalitat de la precipitació i la temperatura. Aquestes condicions defineixen un cert patró de continentalitat on els boixos més susceptibles de ser atacats són aquells que es troben a prop de la costa i a baixa elevació (a les províncies de Girona, Barcelona i Navarra) i excloent zones del Pirineu central (Lleida, Huesca). Les projeccions futures de l'impacte causat per *C. perspectalis* descriuen una relació de consumidor-recurs cíclica amb l'estat dels boixos. A més el canvi climàtic podria reduir l'àrea d'impacte sever causat per l'insecte concentrant-lo només a algunes localitats. La interacció entre *C. perspectalis* i altres pertorbacions com el foc i la sequera extrema no ha resultat significativa. Tot i això, tal com he descrit en altres espècies d'insectes forestals, les interaccions amb altres pertorbacions són complexes i es produeixen en diverses direccions, efectes (antagònic i sinèrgic) i escales espacials i temporals. Per exemple s'han revisat estudis sobre arbres que quan estan danyats pel foc o per sequera sintetitzen etanol, monoterpens i feromones que atrauen als insectes; els arbres morts per causa d'una plaga d'insectes impliquen una acumulació de combustible que facilita la propagació d'incendis; els arbres debilitats per la sequera tenen una capacitat de resposta (síntesi de resines, capacitat de rebrot, etc.) menor i per tant són més susceptibles als atacs d'insectes; etc. Tota aquesta informació ofereix una base de gran valor per a la futura recerca i pel disseny d'estratègies de gestió de boscos i plagues.

Introduction to the subject

Forest insects as landscape biotic drivers

Insects are key drivers of change in landscape ecosystems around the world (FAO 2008). They are integrated components of forests dynamics, although they may lead severe disturbances compromising growth and viability of their host trees. For instance, insects may drive forest succession by disturbing only pioneer species and speeding up the process towards later development stages (Berryman 1986). Other studies have documented that some conifers have co-adapted to the bark beetle *Scolytus ventralis* LeConte, becoming susceptible to attacks at an age that maximizes their offspring's success (Raffa and Berryman 1987). Insects also alter forest productivity because they are usually more successful at attacking and reproducing on trees that are under the greatest stress, regulating the recycling process of nutrients that are used by healthy trees to grow. Besides, borers and defoliator insects play an essential role in food web as primary consumers of vegetal tissues not profitable by other species, as in the case of spruce budworm (*Choristoneura fumiferana* Clem.), causing a birdfeeder effect and corresponding to a cascade of increasing diversity and food-web complexity (Eveleigh et al. 2007). Forest insects play other functions in the ecosystem including their role as pollinators, as pathogen vectors that accelerate the decomposition of dead wood, etc. (Berryman 1986; FIG 1).

However, insect may cause a decay on host plant growth, limit its regenerative capability, and compromise its viability. When this impact is continued and/or accentuated it may lead to important ecological, economic, and cultural impacts. Ecological impacts include losses in the biodiversity, since insect disturbances indirectly influence other species living in the ecosystem altered (Kenis et al. 2009; FIG 1). This is the case of the dramatic mortality observed in Fraser fir (*Abies fraseri* Pursh) and Eastern hemlock (*Tsuga canadensis* L.) due to *Adelges* spp. that has totally altered forest plant communities in eastern USA (Eschtruth et al. 2006). Furthermore, some insects act as vectors or facilitators of other forests diseases that disturb ecosystems incrementing the mentioned consequences (Brasier, 2000). Insect attacks may alter tree reproduction, transpiration and growth processes, modifying forest productivity and, consequently, its economic performance in the case of managed forests. It has been reported that insect pests impact 35 M hectares worldwide (van Lierop et al. 2015), and this represents almost US $10,000 M of annual costs including management costs, losses in forest market, and in



▶ **FIGURE 1**
Role of insects on forest dynamics when are in equilibrium in the ecosystems (upper panel). Human activity lead to severe insect pest episodes and increase the impact on forests (low panel).

non-market values (i.e., recreation, aesthetics, and homeowner benefits of property; (Rosenberger et al. 2015; Diagne et al. 2021). Finally, the cultural consequences of forest pests when impacting species or regions of high interest should also be considered. For example, in North America, the loss of the Black ash (*Fraxinus nigra* Marshall) due to emerald ash borer (*Agrilus planipennis* Fairmaire) impacts on the traditional basket making carried out by the Native North Americans (Diamond and Emery 2011; Willow 2011; Reo 2012).

Insect pests and global change in the Anthropocene

Insect pests have shaped ecosystems for ages. They are already mentioned in the biblical texts (Ex. 10:1-20) and considered problems for the economy in European informs of the 17th century (Azcarate Luxán 1996). However, there has been an increase of the frequency and severity of insect pest episodes during the last decades, as a direct and/or indirect consequence of human activity (Hulme 2009; Ayres and Lombardero 2018). In the current age named Anthropocene (Crutzen

2006), climate change, the increasingly intensive human land use and the propagation of nonnative species have led the current dynamics of insect pests (FIG. 1).

As a feature of land use changes, there are millions of hectares of productive forests around the world that involve monocultures of nonnative tree species (Ayres and Lombardero 2018). Although the use of nonnative tree species is motivated to optimize production and avoid tree natural herbivores and pathogens, the lack of enemies can also work to the benefit of nonnative herbivores when they arrive and cause severe impacts on cultivated trees (Elton, 1958). For example, Sirex wood wasps (*Sirex noctilio* F.), which are native to Europe, (Lombardero et al. 2012), have become an enormous pest for pine plantations in the Southern Hemisphere following their accidental introduction via wooden shipping materials (Slippers et al. 2012). Also, invasive *Gonipterus* spp. beetles, native to Australia, are challenging the viability of eucalyptus production forests on every continent where the tree species is introduced for cultivation (Reis et al. 2012). Habitat configuration as a consequence of land use changes also influences insect dynamics. Landscape management leads to greater forest fragmentation around the world, which impacts the biodiversity and behavior of the species that live in there (Roland 1993; Riitters et al. 2000). In the case of forest insects, there are cases documenting an Allee effect in how habitat fragmentation implies a decay of insect performance (Barron et al. 2020), while other studies demonstrate that insects perform better at the edges of forest patches, which are favored by forest fragmentation (Samalens and Rossi 2011).

Climate change modifies the distribution and phenology of multiple species, including insects and plants, as well as the insect-host relationship. For instance, climate warming has permitted *Dendroctonus* bark beetles and the processionary moth (*Thaumetopoea pityocampa* D. and Shiff) to expand their ranges into conifer forests at higher latitudes and elevations that just few decades ago were protected by temperatures too cold for the winter-feeding larvae (Battisti et al. 2005; Bentz et al. 2010; Weed et al. 2013). Rising temperatures and changes in degree-days modify insect phenology by regulating its diapause and increasing the number of generations per year (known as voltinism; Forrest 2016; Suppo et al. 2020). This was observed in different species of the genus *Dendroctonus* in North America, where an increase in the number of generations per year led to longer insect feeding season and, consequently, to a more severe impact to the forest (Bentz et al. 2010; Mitton and Ferrenberg 2012; Everall2015). Moreover, climate change may lead to the loss of climatic suitability of the host plant, causing its decline and a lower response capacity to insect attacks. Thus, the severity of insect pest damage depends on both the insect fitness and the response of their hosts (Hart et al. 2014;

Sangüesa-Barreda et al. 2015). However, it is necessary to emphasize that new climatic conditions do not always favor the spread and virulence of insect pests. In some cases, climate suitability of insect species is reduced under changing conditions, leading to a transition or reduction in the distribution area (Bebber et al. 2013; Grünig et al. 2020). Other studies propose that water stress reduces the vulnerability of trees to insect attack because of the less hospitable environment that insects experience in a drought-stressed tree (Kolb et al. 2016).

Biological invasions

Biological invasions also contribute to an increase of the insect pest impacts. Such invasions progress through four consecutive phases: *a*) introduction, *b*) establishment, *c*) spread, and *d*) impact (Vermeij 1996; Blackburn et al. 2011). Species in this process are known as *alien* species (also referred to as *introduced* or *non-native*) and only those that reach the spread and impact stages are considered *invasive* (Blackburn et al. 2011).

During the last 20 years we have witnessed an increase in biological invasions and in the research focusing on it. But in general, the movement and introduction of species (stage *a*) has been linked to human activity for millennia due to international trade that favors the accidental introduction of species into new ecosystems (Hulme 2009; Bradshaw et al. 2016). In fact, defining moments in biological introductions are linked with the European arrival to America (15th century), the Industrial Revolution (19th century), the European migrations between 1820 and 1930, and, most remarkably, the recent era of market globalization (Hulme 2009). This trend is more notorious in countries with high economic activity, large transport infrastructure, and facilitators of international trade, an idea that is exemplified in that the Gross Domestic Product of different countries was found to correlate with the richness of alien species (Kobelt and Nentwig 2008).

New climatic conditions are also described as a key factor in the increase of alien species and its probability to establish, spread and impact new locations (stages *b*, *c*, and *d*; Dukes and Mooney 1999; FAO 2008). In general, invasive species share traits such as short generation times, rapid dispersal, or environmental plasticity that could be advantageous in a transitioning climate (Dukes and Mooney 1999). However, as mentioned in the section above, climate change does not always lead to a climatic-niche widening of the introduced species.

Indeed, climate influence varies according to taxon, species, and potential areas of invasion (Eaton and Scheller 1996; Peterson et al. 2008). This is the case of the Argentinian ant (*Linepithema humile* Mayr), whose area of suitable climate is predicted to retract in the tropical regions, but expand at higher latitudes (Roura-Pascual et al. 2005).

In the case of invasive forest insects, their direct ecological consequences are related to genetic hybridization with native species and to competition for resources with native herbivores. Indirect impacts encompass their role as plant and insect vector diseases, and, more important in the case of forest outbreaks, severe defoliation of native forest species and related impacts (Kenis et al. 2009; Blackburn et al. 2014). There are multiple examples of defoliation by invasive insects, but probably one of the best studied is the case of the gypsy moth (*Lymantria dispar* L.), native from Europe and introduced in North America in the 19th century, becoming the main pest of broadleaved trees in Eastern North America. Repeated defoliation may lead to severe tree mortality, particularly in oak (*Quercus* spp.) stands (Kenis et al. 2009). Since then, the costs associated with the damage caused by this pest and its management range between US $10-25 M (Tobin et al. 2012; Diagne et al. 2021). This opens the debate on which management of invasive insects is appropriate considering their economic, ecological, and cultural costs. Blackburn et al. (2011) proposed that intervention time is key to pest management, and that with each change of stage, management strategies must be adapted: prevention is necessary to avoid the introduction of alien species; once introduced, efforts must be focused in eradicating them; finally, if the species is in the dispersal phase it will be necessary to implement containment and mitigation measures.

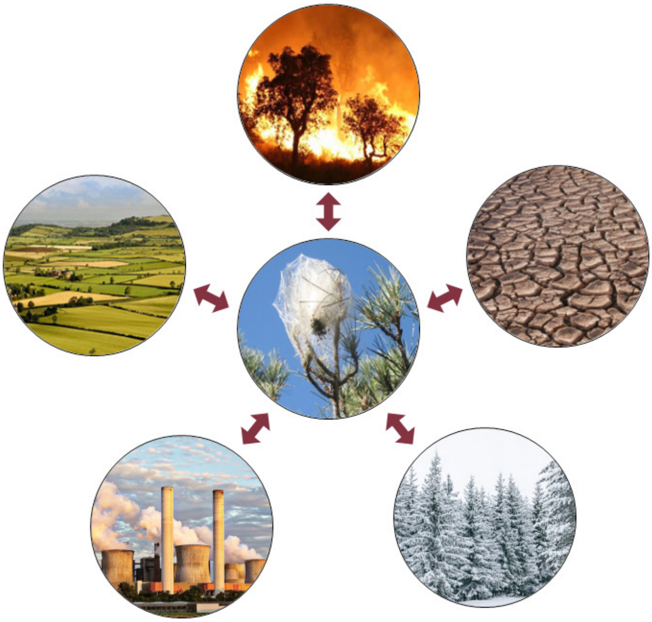
Interaction between insect pests and other forest disturbances

Direct effects of insect pests on forests have been exposed in the text above. However, insect pests indirectly drive forest landscape dynamics via the interaction with other disturbances such as fire, windstorms, or drought. These disturbances both drive and are driven by landscape dynamics, so it is commonly reported that the consequences of one disturbance in the landscape alter the likelihood or behavior of a later one. Moreover, an increase in disturbance occurrence and severity has been documented in the recent decades over the globe due to a combination of land-use changes, human-induced climate warming, and changes in disturbance management, leading to more frequent and new disturbance interactions (Seidl et al. 2017). Thus, the study of landscape disturbances is getting more complex and requires studying not only the individual behavior of each one, but also the interaction between them (Turner and Gardner 2015).

In the case of insect outbreaks interacting with other disturbances, a complex net of involved processes has been reported (FIG . 2). Insect pests may influence and be influenced by fire, drought, windstorms, forest management, pollution, and other pests or diseases impacting forests. For instance, it has been broadly described how insect pests modify the accumulation of fuel and consequent wildfire susceptibility and severity (McCullough et al. 1998; Parker et al. 2006; Jenkins et al. 2014; Meigs et al. 2015; James et al. 2017). Or conversely, Kelsey et al., (2014, 2011) proposed that trees that are stressed by fire, drought or pests generate more ethanol, monoterpenes sugars, and pheromones that attracts new insects. Even less studied disturbances such as windstorms, landslides or snow avalanches may influence insect dispersion, tree susceptibility or forest structure in general that favor insect attacks (Hanewinkel et al. 2008; Simard and Lajeunesse 2015; Havašová et al. 2017).

Catalonia and insect pests

In this study I used the Southern Pyrenees and, more specifically, Catalonia as an area to analyze the impact of insect pest outbreaks on forest landscape (FIG . 3). Catalonia is a Mediterranean region of about 32,000 km2 located in northeastern Spain, with high population density (242 inhabitants per km2 in 2019). Its complex orography, with an altitude range from 0 to more than 3,000 m above sea level and a lineal coast extending over 750 km, results in highly diverse climate and vegetation patterns. Catalonia landscapes encompass diverse mosaics of agricultural plains, pine-oak forests and mountainous shrublands. Sixty percent of the area is covered by forests and shrublands, the third most forested area in Europe (Ibàñez et al. 2002). Dominant tree species are pines (*Pinus halepensis*, *P. nigra*, *P. sylvestris*, *P. uncinata* and *P. pinea*) and Holm oaks (*Quercus ilex* and *Q. suber*). The understory is highly heterogeneous and usually rich in helio-xerophytic species including *Q. coccifera*, *Rosmarinus officinalis*, *Erica multiflora*, *Cistus* spp., etc. in Mediterranean forests and *Buxus sempervirens* in limestone of sub-Mediterra-



▶ **FIGURE 2**
Main interactions between insect pests and other forest disturbances such as fire, drought, storms, pollution, and land use changes.

▶ **FIGURE 3**
Location of Catalonia (in black) and Southern Pyrenees (dark grey) in the European context.

nean and sub-alpine environments (Villanueva 2005). Shrublands are dominated by *R. officinalis*, *Thymus vulgaris*, *Globularia alypum* and *Q. coccifera*.

The study of insect pests in Europe is relatively young and less developed than the study of agricultural pests, due to its lower economic value. The first European publication on forest entomology is dated in 1752 by the parish priest of Regenesburg, J. C. Schäffer, specifically on *L. dispar* (Azcarate Luxán 1996). In Catalonia, there are some publications of agricultural pests from the 18th century, as in the case of locust pest (*Dociostaurus maroccanus*, Thunb.) and especially the phylloxera (*Daktulosphaira vitifoliae*, Fitch) which destroyed 385,000 ha of vineyards in the region between the end of the 19th and beginning of 20th centuries (Piqueras Haba 2005). The first report on forest insect pests was written at the end of the 19th century, also describing the affectation of *L. dispar* on oaks and cork oaks (*Quercus* spp.) of Girona region (NE Catalonia). Other reports published in that period mentioned the impact of the flathead oak borer (*Coraebus undatus*, F.) and the wood ant (*Formica rufa* L.) on cork oaks (Azcarate Luxán 1996). These species still have significant impacts on Catalan forests today, while other species have increased its scientific interest (TABLE 1). Currently, main insects impacting *Quercus* spp. are *L. dispar*, *C. undatus*, *Tortrix viridana* L., and *Kermes vermilio* Planch. The main insects impacting conifers are *T. pityocampa*, *Tomicus* spp., and *L. monacha* L. (TABLE 1)

T. pityocampa has been the main defoliating insect in Catalan forests during the last years, focusing the concern of society, forest owners and forest managers. This native Lepidoptera causes severe defoliation on pines, mainly on tenderest leaves, during its larval stage from October to February (Battisti et al. 2005). Although defoliation due to the processionary moth does not induce the host tree death, it causes weakness that may result fatal in the face of other disturbances such as drought, or consecutive pest outbreaks. The population dynamics of the pine processionary is described as cyclical, with severe episodes every 5-6 years (Hódar and Zamora 2004; Robinet et al. 2007). However, during recent years, this pest has impacted more severely and in more areas of the region. Climate change is pushing favorable conditions for the development of the moth and in particular increasing winter temperatures, which is considered the main constraint for its survival (Battisti et al. 2006; Hódar and Zamora 2012). Changing weather conditions leads the pine processionary to reach new areas and higher elevations where it was not previously found. Because the larval stinging is dangerous for human and pets and because its important landscape impact, management of the pine processionary is performed every year through the use of pheromone traps and pesticides by local and regional governments.

Management of other insect pests in Catalonia includes measures such as monitoring populations by pheromone traps, forest management to prevent focus of infection, and phytosanitary control by spraying of *Bacillus thuringensis* (a bacterium that causes the collapse of the digestive system of many species of lepidoptera, dipterans, coleoptera and hymenoptera) from trunks, planes, or helicopters. However, management of these species is controversial, especially when using pesticides, and an example is the case of *L. dispar*. This species dynamics is described as cyclic involving more severe attacks every 7-9 years (Allstadt et al. 2013), causing a high impact on the media and on the popular opinion. On the one hand, the market of timber and cork is damaged by the pest, and forest owners are demanding quick and efficient treatments. On the other hand, the use of pesticides such as *B. thuringensis* is rejected by part of the population and scientific community, as this bacterium may not always be effective at landscape scales and it is not specialist on *L. dispar* so that it can compromise insect biodiversity in fumigated areas. Finally, there is an unequal awareness of the population regarding pest control, which is biased by the popularity of some species/areas but is not based on the ecological processes involved.

Catalonia and a broader region of the Southern Pyrenees have a high degree of anthropization and tourism activity and are placed in an important point for both land and sea transport. These areas have suffered a major land transformation in recent years leading to an increase in habitat fragmentation. All these characteristics, together combined with the climatic heterogeneity of the area, have historically favored the introduction and establishment of non-native species (Pino et al. 2005). The list of invasive species in Catalonia exceeds 1700 species (Andreu and Pino 2013), and the main insects that cause damage to the forest landscape are: the western conifer seed bug (*Leptoglossus occidentalis* H.), an hemipter native to the western USA present in Catalonia since 2004 (Ribes and Escolà 2005) that feeds on tender shoots and pine cones; beetles of the genus *Monochamus* with non-European origin, which cause damage as facilitators of the nematode *Bursaphelenchus xilophilus* and cause the sudden decay of pines; and, more recently, the box tree moth, *Cydalima perspectalis* W (TABLE 1).

The tree box moth *C. perspectalis* (Lepidoptera: Crambidae) is a native insect from Asia and was introduced in Europe in 2007 (Germany) via the trade of ornamental box trees (Leuthardt 2013; Nacambo et al. 2014). In recent years, new observations have been recorded in Switzerland and the Netherlands (Straten and Muus 2010; Leuthardt 2013), and in a period of 10 years, the insect has spread across Europe and into Asia Minor (Bras et al. 2019). In Europe, *C. perspectalis* is hosted on *Buxus sempervirens* L., and its larvae feed on boxwood leaves, leading to complete defoliation and dead of the host plant. However, the resprout ability of boxwood plants and their survival capacity after consecutive defoliation episodes are still unknown (Artola 2019). Distribution and impact of the box tree moth seems to be restricted by the presence of its host plant and by climate, that influences the diapause and larval development (Nacambo et al. 2014). In Catalonia, *C. perspectalis* was first identified in 2014 in Girona, and since then it has spread across the boxwood distribution (Bassols and Oliveras 2014). Management of this species is complicated because of large knowledge gaps on its biology, its ecological/climatic niche, the processes of interaction with new competitors and predator species, and the long-term effects to the invaded landscape.

The arrival of this new invasive species compromising rich forest landscape means an ideal context for the study of insect pest outbreaks to Mediterranean integrated landscape, the role of the interactions between insect pests and other disturbances and the projection of the dynamics of an invasive species using landscape simulation models.

	NAME	**TAXONOMY**	**HOST PLANT**	**IMPACT**	**MANAGEMENT TECHNIQUES USED**
NATIVE SPECIES	Gypsy moth (*Lymantria dispar*)	Lepidoptera	*Quercus suber, Q. ilex.*	Foliage feeder that causes severe defoliations modifying the seed, wood, and cork production.	Favoring predatory birds and use of pheromone traps. The use of pesticides is only recommended in extreme cases.
	Flathead oak borer (*Coraebus undatus*)	Coleoptera	*Q. suber*	Xylem feeder that borers bark damaging cork use and market.	Use of pheromone and chromatic traps.
	Green oak tortrix (*Tortix viridana*)	Lepidoptera	*Q. suber,* *Q. pubsecens,* *Q. ilex*	Foliage feeder that causes severe defoliations influencing tree growth, seed productions and leading to tree dead.	Naturally controlled by birds and parasites.
	Kermes vermilio	Hemiptera	*Q. ilex,* *Q. coccifera* and other *Quercus*	Sap feeder that produces damages on leaves, drying of twigs and reduction of shoots.	Naturally controlled by parasites and entomopathogens fungi.
	Pine processionary (*Thaumetopoea pityocampa*)	Lepidoptera	*Pinus nigra,* *P. sylvestris,* *P. radiata, P. canariensis* and other *Pinus* and *Cedrus.*	Foliage feeder that causes severe defoliation on the host trees influencing tree growth and inducing other biotic attacks. Caterpillars are stinging to people and pets.	Forest management to avoid insect focus of infection, removal of nests, use of pesticides, pheromone traps
	Pine beetles (*Tomicus piniperda,* *T. minor,* *T. destruens*)	Coleoptera	*Pinus spp.*	Xylem feeders influencing tree growth, leaves and wood production and leading to tree decay and dead.	Forest management to avoid insect focus, food traps. The use of pesticides is only recommended in extreme cases.
	Nun moth (*Lymantria monacha*)	Lepidoptera	*Pinus sylvestris* and other *Pinus, Abies* and *Picea*	Foliage feeder causing tree decay and other biotic attacks.	Monitoring of the species and use of pesticides.

	NAME	**TAXONOMY**	**HOST PLANT**	**IMPACT**	**MANAGEMENT TECHNIQUES USED**
ALIEN SPECIES	Western conifer seed bug (*Leptoglossus occidentalis*)	Hemiptera	*P. halepensis, P. pinea, P. sylvestris, P. nigra* and other *Pinus.*	Seed feeder, causing problems with seed production and fitness.	Monitoring of the species.
	Monochamus spp.	Coleoptera	*Pinus* spp.	Xylem feeder that borer dead or dying trees and acting as facilitators of the nematode Bursaphelenchus xilophilus causing the sudden decay of pines	-
	Box tree moth (*Cydalima perspectalis*)	Lepidoptera	*Buxus sempervirens*	Foliage feeder that defoliates box tree causing a decay or even the dead of the host plant.	Monitoring of the species, pheromone traps.

▶ TABLE 1
Summary of the main forest insect pests in Catalonia, both native and alien species.

Objectives and thesis structure

The general goals of this thesis are to offer new visions in the insect pests and their impacts on forest landscape, to explore current and future interactions between insect pests and other disturbances, and to offer novel modelling approaches to describe and anticipate insect dynamics. The combined use of Species Distribution Models, spatially explicit landscape simulation models and the comprehensive discussion of insect impacts integrated on disturbed landscapes aim at informing management policies and aspire to create the basis for further research.

THE SPECIFIC AIMS OF THE THESIS ARE:

+ To evaluate insect pests as a key driver of landscape dynamics.

+ To analyze the role of climate change on the dynamics of insect pest outbreaks.

+ To describe the direct and indirect impacts of insect pests on forest systems and their interactions with other disturbances.

+ To anticipate the future potential interaction between insect pests and other disturbances under a global change scenario.

+ To introduce new modelling methodologies that simulates alien species distribution and impact.

+ To explore different modelling tools for the study of landscape dynamics.

+ To offer a theoretical context to base management strategies.

STRUCTURE

This thesis starts with a general introduction which aims to present the general state of the art on insect pest research, highlight the relevance of this topic on current forest ecology sphere, and point to the main challenges faced by management and research under the current global change situation. Then, I aimed to respond the questions mentioned above through the following tree chapters:

In Chapter 1 I conducted an exhaustive scientific literature review about the interaction between insect pests and other forest disturbances such as fire, drought, pollution, or storms. To select the final set of 216 scientific articles, I fulfilled a systematic review using specific keywords on different platforms. I described a complex net of forest interactions through different spatio-temporal levels, and I concluded that simulation models are key tools to study their dynamics. This chapter is a convenient summary of insect pest consequences beyond its direct effects and establishes the basis for further research.

Cydalima perspectalis, native from Asia, arrived in Catalonia in 2014 and in 2017 severely impacted boxwoods in the region. In Chapter 2 I used this species as a prime example of forest insect pest. I modelled its climatic and ecological niche and projected its spread and impact across the study area. Because this is an alien species in Europe, modeling its suitability required the use of data from the native and the invaded area.

In Chapter 3 I analyzed *Buxus sempervirens* viability in Southern Pyrenees (Spain) facing fire, drought, and *C. perspectalis* pest disturbances. I projected landscape dynamics for the period 2020-2080 through the design and use of a landscape simulation model. I evaluated different climatic scenarios and the interaction between insect pests and the other disturbances. This chapter compiles information presented in the previous two, highlighting the use of simulation models to study the impact of insect pests and its interactions on forest landscapes.

Finally, I discuss the main findings and contributions of this thesis while the main concluding remarks are exposed in the last section.

References

Allstadt AJ, Haynes KJ, Liebhold AM, Johnson DM (2013) Long-term shifts in the cyclicity of outbreaks of a forest-defoliating insect. *Oecologia* 172:141–151. https://doi.org/10.1007/s00442-012-2474-x

Andreu J, Pino J (2013) El projecte EXOCAT. Informe 2013. 111

Artola J (2019) Seguiment de la biologia i la fenologia de la papallona del boix (*Cydalima perspectalis*) al Parc Natural de la Sona Volcànica de la Garrotxa. General Cataluna; *Dep Territ i Sostenibilitat*

Ayres MP, Lombardero MJ (2018) Forest pests and their management in the Anthropocene. *Can J For Res* 48:292–301. https://doi.org/10.1139/cjfr-2017-0033

Azcarate Luxán I (1996) Plagas agrícolas y forestales en España (siglos XVIII y XIX)

Barron MC, Liebhold AM, Kean JM, et al (2020) Habitat fragmentation and eradication of invading insect herbivores. *J Appl Ecol* 57:590–598. https://doi.org/10.1111/1365-2664.13554

Bassols E, Oliveras J (2014) *Cydalima perspectalis* (Walker , 1859), una nova espècie invasora a Catalunya (Lepidoptera) *Butll Soc Cat Lep* 105:71–78

Battisti A, Stastny M, Buffo E, Larsson S (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Glob Chang Biol* 12:662–671. https://doi.org/10.1111/j.1365-2486.2006.01124.x

Battisti A, Stastny M, Netherer S, et al (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Appl Sci* 15:2008–2009

Bebber DP, Ramotowski MAT, Gurr SJ (2013) Crop pests and pathogens move polewards in a warming world. *Nat Clim Chang* 1–4. https://doi.org/10.1038/NCLIMATE1990

Bentz BJ, Régnière J, Fettig CJ, et al (2010) Climate change and bark beetles of the Western United States and Canada: Direct and indirect effects. *Bioscience* 60:602–613. https://doi.org/10.1525/bio.2010.60.8.6

Berryman AA (1986) Insects in the Forest Environment. In: Forest Insects Principles and Practice of Population Management. *Plenum Press*, New York, pp 33–50

Blackburn TM, Essl F, Evans T, et al (2014) A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biol* 12:. https://doi.org/10.1371/journal.pbio.1001850

Blackburn TM, Pyšek P, Bacher S, et al (2011) A proposed unified framework for biological invasions. *Trends Ecol Evol* 26:333–339. https://doi.org/10.1016/j.tree.2011.03.023

Bradshaw CJA, Leroy B, Bellard C, et al (2016) Massive yet grossly underestimated global costs of invasive insects. *Nat Commun* 7:. https://doi.org/10.1038/ncomms12986

Bras A, Avtzis DN, Kenis M, et al (2019) A complex invasion story underlies the fast spread of the invasive box tree moth (*Cydalima perspectalis*) across Europe. *J Pest Sci* (2004) 92:1187–1202. https://doi.org/10.1007/s10340-019-01111-x

Crutzen PJ (2006) The anthropocene. In: Earth System Science in the Anthropocene. *Springer*, Berlin, Heidelberg, pp 13–18

Diagne C, Leroy B, Vaissière A-C, et al (2021) High and rising economic costs of biological invasions worldwide. *Nature*. https://doi.org/10.1038/s41586-021-03405-6

Diamond AK, Emery MR (2011) Black Ash (*Fraxinus nigra* Marsh.): Local Ecological Knowledge of Site Characteristics and Morphology Associated with Basket-Grade Specimens in New England (USA). *Econ Bot* 65:422–426. https://doi.org/10.1007/s12231-011-9174-z

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *TREE* 14:135–139. https://doi.org/https://doi.org/10.1016/S0169-5347(98)01554-7

Eaton JG, Scheller RM (1996) Effects of climate warming on fish thermal habitat in streams of the United States. *Limnol Ocean* 41(5), 1109-1115.

Eschtruth AK, Cleavitt NL, Battles JJ, et al (2006) Vegetation dynamics in declining eastern hemlock stands: 9 Years of forest response to hemlock woolly adelgid infestation. *Can J For Res* 36:1435–1450. https://doi.org/10.1139/X06-050

Eveleigh ES, McCann KS, McCarthy PC, et al (2007) Fluctuations in density of an outbreak species drive diversity cascades in food webs. *Proc Natl Acad Sci U S A* 104:16976–16981. https://doi.org/10.1073/pnas.0704301104

FAO (2008) Salud y vitalidad de los bosques. 69–88

Forrest JR (2016) Complex responses of insect phenology to climate change. *Curr Opin Insect Sci* 17:49–54. https://doi.org/10.1016/j.cois.2016.07.002

Grünig M, Calanca P, Mazzi D, Pellissier L (2020) Inflection point in climatic suitability of insect pest species in Europe suggests non-linear responses to climate change. *Glob Chang Biol* 26:6338–6349. https://doi.org/10.1111/gcb.15313

Hanewinkel M, Breidenbach J, Neeff T, Kublin E (2008) Seventy-seven years of natural disturbances in a mountain forest area - the influence of storm, snow, and insect damage analysed with a long-term time series. *Can J For Res* 38:2249–2261. https://doi.org/10.1139/X08-070

Hart SJ, Veblen TT, Eisenhart KS, et al (2014) Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* 95:930–939. https://doi.org/10.1890/13-0230.1

Havašová M, Ferenčík J, Jakuš R (2017) Interactions between windthrow, bark beetles and forest management in the Tatra national parks. *For Ecol Manage* 391:349–361. https://doi.org/10.1016/j.foreco.2017.01.009

Hódar JA, Zamora R (2012) Influencia de los factores abióticos y bióticos en la defoliación por la procesionaria del pino (*Thaumetopoea pityocampa*) en los pinares andaluces. *5CFE* XXXIII:81–87. https://doi.org/10.1007/s13398-014-0173-7.2

Hódar JA, Zamora R (2004) Herbivory and climatic warming: A Mediterranean outbreaking caterpillar attacks a relict, boreal pine species. *Biodivers Conserv* 13:493–500. https://doi.org/10.1023/B:BIOC.0000009495.95589.a7

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *J Appl Ecol* 46:10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Ibàñez JJ, Burriel JA, Pons X (2002) El Mapa de Cobertes del Sòl de Catalunya: Una eina per al coneixement, la planificació i la gestió del territori. *Perspect Territ* 10–25

James PMA, Robert LE, Wotton BM, et al (2017) Lagged cumulative spruce budworm defoliation affects the risk of fire ignition in Ontario, Canada: *Ecol Appl* 27:532–544. https://doi.org/10.1002/eap.1463

Jenkins MJ, Runyon JB, Fettig CJ, et al (2014) Interactions among the mountain pine beetle, fires, and fuels. *For Sci* 60:489–501

Kelsey RG, Gallego D, Sánchez-García FJ, Pajares J a. (2014) Ethanol accumulation during severe drought may signal tree vulnerability to detection and attack by bark beetles. *Can J For Res* 44:554–561. https://doi.org/10.1139/cjfr-2013-0428

Kelsey RG, Joseph G, McWilliams MG (2011) Ethanol synthesis by anoxic root segments from five cedar species relates to their habitat attributes but not their known differences in vulnerability to Phytophthora lateralis root disease . *Can J For Res* 41:1202–1211. https://doi.org/10.1139/x11-043

Kenis M, Auger-Rozenberg M-A, Roques A, et al (2009) Ecological effects of invasive alien insects. *Biological invasions*, 21–45. https://doi.org/10.1007/s10530-008-9318-y

Kobelt M, Nentwig W (2008) Alien spider introductions to Europe supported by global trade. *Divers Distrib* 14:273–280. https://doi.org/10.1111/j.1472-4642.2007.00426.x

Kolb TE, Fettig CJ, Ayres MP, et al (2016) Observed and anticipated impacts of drought on forest insects and diseases in the United States. *For Ecol Manage* 380:321–334. https://doi.org/10.1016/j.foreco.2016.04.051

Leuthardt FLG (2013) Distribution , life history , food choice and chemical ecology of the invasive box-tree pyralid *Cydalima perspectalis*. *University of Basel*

Lombardero MJ, Alonso-Rodríguez M, Roca-Posada EP (2012) Tree insects and pathogens display opposite tendencies to attack native vs. non-native pines. *For Ecol Manag*e 281:121–129. https://doi.org/10.1016/j.foreco.2012.06.036

McCullough DG, Werner RA, Neumann D (1998) Fire and insects in northern and boreal forest ecosystems of North America. *Annu Rev Entomol* 43:107–127. https://doi.org/10.1146/annurev.ento.43.1.107

Meigs GW, Campbell JL, Zald HSJ, et al (2015) Does wildfire likelihood increase following insect outbreaks in conifer forests? *Ecosphere* 6:art118. https://doi.org/10.1890/ES15-00037.1

Mitton JB, Ferrenberg SM (2012) Mountain pine beetle develops an unprecedented summer generation in response to climate warming. *Am Nat* 179:. https://doi.org/10.1086/665007

Nacambo S, Leuthardt FLG, Wan H, et al (2014) Development characteristics of the box-tree moth *Cydalima perspectalis* and its potential distribution in Europe. *J Appl Entomol* 138:14–26. https://doi.org/10.1111/jen.12078

Parker TJ, Clancy KM, Mathiasen RL (2006) Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agric For Entomol* 8:167–189. https://doi.org/10.1111/j.1461-9563.2006.00305.x

Peterson AT, Stewart A, Mohamed KI, Arau MB (2008) Shifting Global Invasive Potential of European Plants with Climate Change. *PLoS One* 3:1–7. https://doi.org/10.1371/journal.pone.0002441

Pino J, Font X, Carbó J, et al (2005) Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). *Biol Conserv* 122:339–350. https://doi.org/10.1016/j.biocon.2004.08.006

Piqueras Haba J (2005) La filoxera en España y su difusión espacial: 1878-1926. *Cuad Geogr* 101–136

Raffa KF, Berryman AA (1987) Interacting selective pressures in conifer- bark beetle systems: a basis for reciprocal adaptations? *Am Nat* 129:234–262. https://doi.org/10.1086/284633

Reis AR, Ferreira L, Tomé M, et al (2012) Efficiency of biological control of *Gonipterus platensis* (Coleoptera: Curculionidae) by *Anaphes nitens* (Hymenoptera: Mymaridae) in cold areas of the Iberian Peninsula: Implications for defoliation and wood production in Eucalyptus globulus. *For Ecol Manage* 270:216–222. https://doi.org/10.1016/j.foreco.2012.01.038

Reo NJ (2012) Ash trees, indian communities and the emerald ash borer. *SSRN Electron J*. https://doi.org/10.2139/ssrn.1739105

Ribes J, Escolà O (2005) "*Leptoglossus occidentalis*" Heidemann., 1910, hemípter neàrtic trobat a Catalunya (Hemiptera: Heteroptera: Coreidae). *Sess Conjunta d'Entomologia* 13:47–50

Riitters K, Wickham J, Neill RO, et al (2000) Global-scale patterns of forest fragmentation. *Ecol Soc* 4:1–24

Robinet C, Baier P, Pennerstorfer J, et al (2007) Modelling the effects of climate change on the potential feeding activity of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Notodontidae) in France. *Glob Ecol Biogeogr* 16:460–471. https://doi.org/10.1111/j.1466-8238.2006.00302.x

Roland J (1993) Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* 25–30

Rosenberger RS, Bell LA, Champ PA, Smith EL (2015) Nonmarket economic values of forest insect pests: An updated literature review. In: Forest Insect Pests: Literature Review of Nonmarket Economic Impacts. pp 1–83

Roura-Pascual N, Pons P, Etienne M, Lambert B (2005) Transformation of a rural landscape in the Eastern Pyrenees between 1953 and 2000. *Mt Res Dev* 25:252–261. https://doi.org/10.1659/0276-4741(2005)025[0252:TOARLI]2.0.CO;2

Samalens JC, Rossi JP (2011) Does landscape composition alter the spatiotemporal distribution of the pine processionary moth in a pine plantation forest? *Popul Ecol* 53:287–296. https://doi.org/10.1007/s10144-010-0227-4

Sangüesa-Barreda G, Linares JC, Camarero JJ (2015) Reduced growth sensitivity to climate in bark-beetle infested Aleppo pines: Connecting climatic and biotic drivers of forest dieback. *For Ecol Manage* 357:126–137. https://doi.org/10.1016/j.foreco.2015.08.017

Seidl R, Thom D, Kautz M, et al (2017) Forest disturbances under climate change. *Nat Clim Chang* 7:395–402. https://doi.org/10.1038/nclimate3303

Simard M, Lajeunesse P (2015) The interaction between insect outbreaks and debris slides in a glacial valley of the eastern Canadian shield. *Ecosystems* 18:1281–1289. https://doi.org/10.1007/s10021-015-9897-2

Straten MJ Van Der, Muus TST (2010) The box tree pyralid, *Glyphodes perspectalis* (Lepidoptera: Crambidae), an invasive alien moth ruining box trees. In: Proceedings of the Netherlands Entomological Society Meeting.

Suppo C, Bras A, Robinet C (2020) A temperature- and photoperiod-driven model reveals complex temporal population dynamics of the invasive box tree moth in Europe. *Ecol Modell* 432:. https://doi.org/10.1016/j.ecolmodel.2020.109229

Tobin PC, Bai BB, Eggen DA, Leonard DS (2012) The ecology, geopolitics, and economics of managing *Lymantria dispar* in the United States. *Int J Pest Manag* 58:195–210. https://doi.org/10.1080/09670874.2011.647836

Turner MG, Gardner RH, et al. (2015) Landscape ecology in theory and practice: Pattern and process. *Springer*, New York.
van Lierop P, Lindquist E, Sathyapala S, Franceschini G (2015) Global forest area disturbance from fire, insect pests, diseases and severe weather events. *For Ecol Manage* 352:78–88. https://doi.org/10.1016/j.foreco.2015.06.010
Vermeij GJ (1996) An agenda for invasion biology. *Biol Conserv* 78:3–9. https://doi.org/10.1016/0006-3207(96)00013-4
Villanueva JA (2005) Tercer inventario forestal nacional (1997–2007). Minist Medio Ambient ICONA
Weed AS, Ayres MP, Hicke JA, et al (2013) Consequences of climate change for biotic disturbances in North American forests. *Ecol Monogr* 83:441–470. https://doi.org/10.1890/13-0160.1
Willow AJ (2011) Indigenizing invasive species management: Native North Americans and the emerald ash borer (EAB) beetle. *Cult Agric Food Environ* 33:70–82. https://doi.org/10.1111/j.2153-9561.2011.01051.x

→01

CHAPTER 01

Global review on interactions between insect pests and other forest disturbances

Quim Canelles
Núria Aquilué
Patrick M. A. James
Joshua Lawler
Lluís Brotons

This chapter has been published in *Landscape Ecology*
(DOI: 10.1007/s10980-021-01209-7)

Abstract

Forest landscapes worldwide are shaped by abiotic drivers such as fire, windstorms, and drought, but also by biotic drivers like insect pests and pathogens. Although the effects of such drivers on forest dynamics have been studied extensively, knowledge of the interactions between insect pests and other drivers of change is still coarse and fragmented. Indeed, new invasive insect species and global change may lead to novel interactions and produce impacts on forest ecosystems never before experienced. We aimed to review the mechanisms underlying interactions between insect pest outbreaks and other forest disturbances, identify interactions emerging from current disturbance dynamics, and highlight the role of simulation models in exploring these interactions in a dynamic, mechanistic, and spatially explicit manner. We reviewed the state of the science regarding interactions between insect pests and other forest disturbances, collecting a set of 216 scientific articles. Most studies focused on the interaction between insect outbreaks and fire, whereas interactions between insect pests and drought, forest management or forest diseases received much less attention. Although we identified some trends in how interactions were manifested, interactions were not more commonly found at particular spatial or temporal scales. Relatively few studies used simulation models to explore interactions between disturbances and very few studies explored multiple interactions. Interactions between pests and other forest disturbances play critical roles in driving forest dynamics. The effects of these interactions are likely to increase in the face of continuing global change.

KEYWORDS
Simulation modeling; outbreak; fire; drought; climate change; landscape dynamics.

Interactions between insect pests and other forest disturbances play a critical role in driving forest dynamics.

Introduction

Forest disturbances such as fire, drought, windstorms, landslides, disease, and insect outbreaks are key drivers of change in forested landscapes. Disturbances modulate landscape dynamics by modifying forest composition and structure, influencing forest ecosystem functioning and resource availability (Seidl et al. 2017; White et al. 1985), and facilitating adaptation to new environmental conditions (Thom et al. 2017). Despite the essential role that natural disturbances play in forest ecosystem functioning and composition, our understanding of their future impacts remains limited due to the complex feedbacks that exist between disturbances and global change (Dale et al. 2001; Turner 2010). For instance, ongoing changes in the global economy, land use, and climate change may lead to more extreme disturbances (such as windstorms, floods, and wildfires) with yet unknown consequences for forest landscapes (Duane and Brotons 2018; Weed et al. 2013). Such changes may also result in novel disturbance caused by invasive species introduced via international trade (Brockerhoff et al. 2006; FAO 2008; van Lierop et al. 2015).

Insect pests are one of the main agents shaping forest landscapes, affecting almost 35 million hectares annually, mainly in boreal and temperate biomes (van Lierop et al. 2015). Although many native pests and diseases are integral agents of forest ecosystems, high-intensity outbreaks can have adverse effects on tree growth and survival (van Lierop et al. 2015). The extent and subsequent economic and ecological costs of pest outbreaks have increased in recent decades as world trade has facilitated the spread of invasive species (Hulme 2009; Turner 2010).

Insect pests are highly sensitive to global change. New environmental conditions resulting from changes in temperature, precipitation, and drought can alter insect development and reproduction (Ayres and Lombardero 2000; Kingsolver et al. 2011), and hence population dynamics and outbreaks. These changes may also enable native and invasive insect pests to spread to areas currently free of such outbreaks (Cullingham et al. 2011). Changes in land use can also influence insect population distributions and local viability (Rosenberger et al. 2017). Although the impact of direct climate-pest and land-use-pest have been examined, we know less about the indirect consequences of insect pests on forest ecosystems through their interactions with other disturbances (Ayres and Lombardero 2000; Hessburg et al. 2015; Raffa et al. 2008).

A deeper understanding of forest disturbance dynamics and their interactions is required to better forecast how global change will affect forest ecosystems (Buma and Wessman 2011). Insect outbreaks have complex relationships with other disturbances, and can be affected by fire (Chou et al. 2010; Hicke et al. 2012; Jenkins et al. 2014; Parker et al. 2006), drought (Sangüesa-Barreda et al. 2015; Temperli et al. 2015), windstorms (Potterf and Bone 2017; Reyes and Kneeshaw 2008), forest management (Bauce and Fuentealba 2013; Rosenberger et al. 2017), pollution (Agrell et al. 2005; Roth et al. 1998), and other pests or diseases affecting the forest (Borkowski and Skrzecz 2016; Jones et al. 2015). Many studies have explored the interactions between insect pests and other disturbance agents (Agne et al. 2018; Anderegg et al. 2015; Colgan and Erbilgin 2010; Day and Pérez 2013; Gitau et al. 2013; Kolb et al. 2016; Leverkus et al. 2018; Millar and Stephenson 2015). However, to date, no global synthesis exists that integrates such interactions with insect pests across different agents and regions, analyzing how global change may influence these interactions in the near future (Seidl et al. 2011), or how alterations in current ecosystems may lead to novel interaction regimes (Turner 2010). Such a synthesis is challenged by the diversity of insect feeding strategies and outbreak dynamics, the multiple ways in which one can characterize insect outbreaks (e.g., severity, frequency, extent), and the multiple spatiotemporal scales at which disturbance interactions occur (Hanula et al. 2002; Joseph et al. 2001; Kelsey and Westlind 2017a; Meigs et al. 2015, 2016).

Ecological models are essential for improving our understanding of interactions between pests and other disturbances in the face of rapid global change. Although empirical models (based on statistical relationships among drivers and a response variable; TABLE 1) are widely used, they can only model observed dynamics and are therefore limited in their capacity to make predictions in novel contexts. In contrast, simulation models (mechanistic models based on a combination of theoretical understanding and mathematical/empirical information; Gustafson and Keene 2014) can be designed to include the effects of uncertain, multiple interacting disturbances characterized by cumulative effects, non-linear dynamics, cross-scale interactions and, most importantly, with the potential to capture unobserved dynamics (Ager et al. 2007; Baker and Robinson 2010; Clark and Gelfand 2006; James et al. 2011a; Keane et al. 2015; Leite et al. 2018; Maroschek et al. 2015; Taylor et al. 2009). Such simulation models are particularly appropriate methods to assess changes in insect species ranges, predict novel insect outbreaks, and anticipate host-insect relationships under novel environmental conditions (Barbet-Massin et al. 2018; Maino et al. 2016; Taylor et al. 2009).

Here we present a systematic review of spatiotemporal interactions between insect pest outbreaks and other forest disturbances. We aim to: 1) detail the processes that determine how insect pest outbreaks interact with other disturbances, while highlighting the main sources of variability in such interactions; 2) identify current and potential future interactions between insect pests and emerging disturbances in the face of global change; and 3) discuss the role of simulation models as a tool for studying both current and novel forest disturbance interactions.

Methods

We searched for publications that examined interactions between insect pests and other forest disturbances. We used the Web of Science, Scopus, and Google Scholar databases to identify articles published between 1990 and 2019 that contained the following words in the title, abstract, or keyword: (Insect) AND (outbreak* OR defoliat* OR infest* OR pest OR bio* disturb* OR epidemic*) AND (forest* OR tree* OR landscape* OR stand*) AND (*fire* OR *burn* OR *drought* OR *logging* OR forest management OR harvest* OR *wind* OR hurricane OR *snow* OR *storm* OR *flood* OR *slide* OR disease OR *pollution*) AND (interact*).

We defined an interaction between disturbances as a direct or indirect relationship in which one disturbance affects the likelihood, extent, severity, or impacts of another. These effects could be either synergistic (a disturbance favors the likelihood or accentuates the impact of a subsequent disturbance) or antagonistic (a disturbance hinders, reduces, or prevents the likelihood or impact of a subsequent disturbance). We did not explicitly include climate change as a disturbance, but its effect was implicit in the influence of insect pest outbreaks, drought episodes, wildfire, wind, and flooding. Papers that were out of our thematic scope (e.g., studies focusing on agricultural instead of forest pests, or that studied multiple disturbances or climate effects on insect pests but not the interactions between them) were excluded. Finally, we included those articles that considered forest management and silvicultural interventions as drivers of change in forests, but not those that analyzed pest control via forest management. A final pool of 216 papers was selected.

We applied a common analysis scheme to all the reviewed studies. For each paper, we recorded information about the study area (at continental level), insect species examined, feeding guild (*sensu* Coviella and Trumble 1999; Labandeira 2013), disturbance agents involved, occurrence or lack of interaction, order of the disturbances, type of response, methodological approach, spatial and temporal scale, ecological explanation, and inferences regarding possible future trends of the interaction when applicable (TABLE 1). We categorized publications as being either empirical analyses or simulation modeling studies (see TABLE 1; Gustafson and Keene 2014). For simulation modeling studies, we also listed the modeling approach, the explanatory variables, the data source, and the projection scenarios considered. Information about disturbance interaction impacts (including the mechanisms of community between species, the immediate and indirect consequences of the disturbance, possible regeneration after impact, etc.) was not always available in the reviewed papers or was difficult to compare. Thus, we calculated summary statistics (frequencies) regarding the above-mentioned variables as a proxy for the incidence of interactions in ecosystems. Finally, studies that found interactions between disturbances were coded with “1”, and those that failed to find such interactions with “0”. We then used logistic regression analyses with the presence of an interaction as the binary response variable and several predictors considered to influence the disturbance interactions (i.e., disturbance agent, order of the disturbance, type of response, insect feeding guild, spatial scale, and temporal scale) as explanatory variables. Regression models were fitted using the *glm* function in R (R Core Team 2019) and significance level was considered at p-value < 0.05.

Differences in the number of publications on disturbance interaction among continents could reflect either true geographic differences in the frequency of interactions between forest pests and other disturbances, or differences in the general amount of forest research being conducted. To account for such differences, and to control for potential geographic bias, we conducted a second search in the Web of Science looking for publications on forest disturbances, in order to then calculate the ratio (per continent) of articles addressing insect pest interactions with other forest disturbances to articles only addressing forest disturbances.

▶ TABLE 1
Information extracted from the selected articles. The right-hand column lists in detail the different categories into which we classified each study within each information field.

PARAMETER	**CATEGORIES**
Study area	Africa; Asia; Europe; North America; Oceania; South America
Insect species	Genus or species reported
Insect feeding guild	**Xylem/phloem feeders:** insects feeding on the vascular tissue system (e.g., bark beetles). **Foliage feeders:** insects feeding on leaves or needles (e.g., defoliators). **Other:** gall producers, saproxylic feeders, seed feeders, or root feeders.
Disturbance agents	Drought; Fire; Forest management; Landslides; Other pathogen/disease; Pollution; Snowstorm; Wind; Flood.
Occurrence of interaction	**Lack of interaction:** one disturbance has no effect on another. **Occurrence of interaction:** one disturbance affects another **Synergistic:** a disturbance increases the likelihood or impact of a subsequent disturbance. **Antagonistic:** a disturbance reduces the likelihood or impact of a subsequent disturbance.
Order of disturbances	Insect pest later influences another disturbance; Other disturbance later influences insect pest; Insect pest and other disturbance occur at the same time.
Type of response	**Likelihood**: earlier disturbance affects the probability of the later one. **Severity**: earlier disturbance influences the severity or intensity of the later one. **Fitness**: earlier disturbance influences the fitness of later insect pests in terms of reproductive success and progeny survival. **Spread**: earlier disturbance influences later insect spread
Methodological approach	**Empirical model approach**: models assessing statistical relationships, whether causal or not, between two or more variables (also called correlative or phenomenological models). **Simulation model approach**: mechanistic models built on a combination of theoretical understanding and mathematical concepts (also based on empirical information and correlative relationships) to emulate a real life system. Normally, simulation models project results to simulated future conditions. They are also called mechanistic or process-based models.
Temporal scale	Days/months; 1 year; 2-9 years; 10-49 years; 50-99 years; >100 years.
Spatial scale	Physiological level; Tree level (individual); Stand level (microhabitat); Landscape level.
Ecological explanation	Conceptual explanation based on ecological processes that cause the interaction of different disturbances (detailed in Table 2).

Results

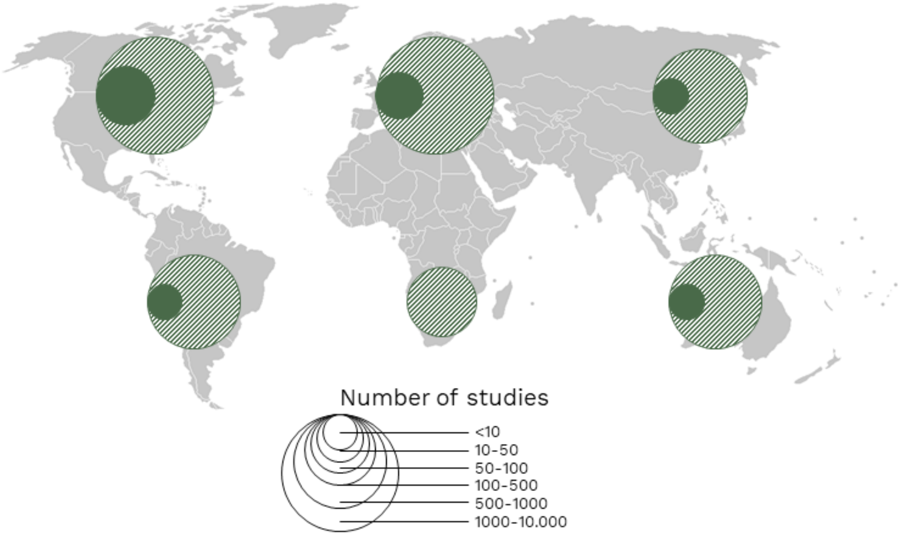
GEOGRAPHIC COVERAGE

Most of the 216 papers reviewed addressed North American forest systems (173; 79%; FIG. 1). Of these papers, most focused on forest insects in western Canada and the USA (133; 61% of the total), followed by Europe (39; 18%). Studies from other continents were very rare and no studies were conducted in Africa.

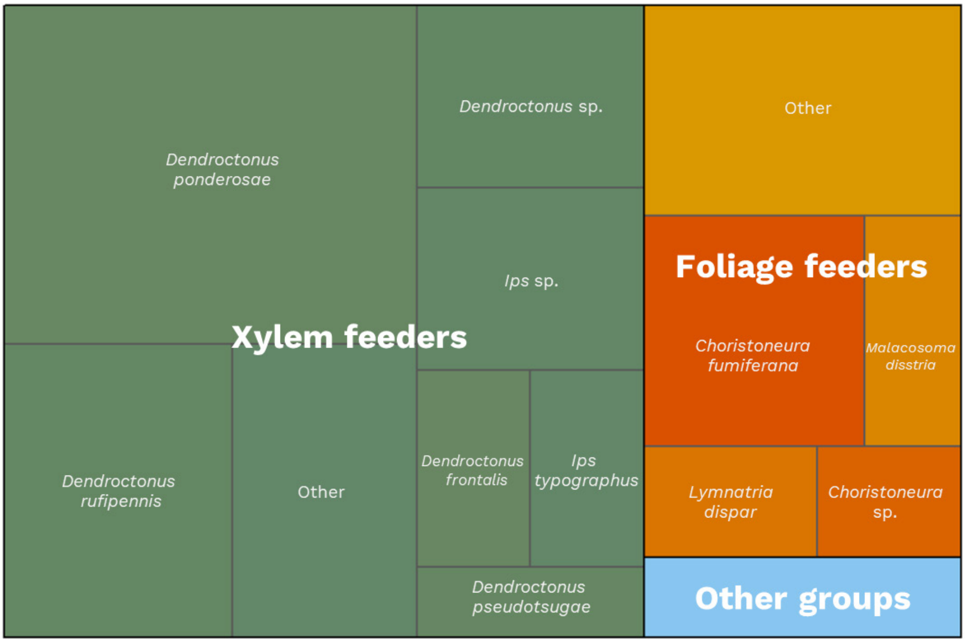
With respect to articles that studied forest disturbances in general (those with and without interactions among disturbances), the greatest number were from North America and Europe (9931; 43% and 7453; 32%, respectively). The proportion of forest disturbance studies that addressed interactions with pests was similarly small across all continents: North America (1.73%), Europe (0.52%), South America (0.16%), Asia (0.13%), Oceania (0.07%), and Africa (0%).

INSECT SPECIES

Xylem and phloem feeders, mainly bark beetles, were the most studied forest insect pests (71%), mainly *Dendroctonus* spp. and *Ips typographus* (FIG. 2). Foliage feeding insects such as defoliating budworms (*Choristoneura* spp.) and gypsy moth (*Lymantria dispar*) (22%), and insects of other feeding groups (7%) were also studied. We also found that interacting disturbance agents varied with insect feeding group: fire, wind, and diseases were usually associated with xylem/phloem feeders (72%, 66%, and 64% over all studies of each disturbance, respectively), pollution was mostly studied in conjunction with foliage feeders (73%). The influence of drought, forest management, and other disturbances (landslides, floods, etc.) was considered across most feeding groups.



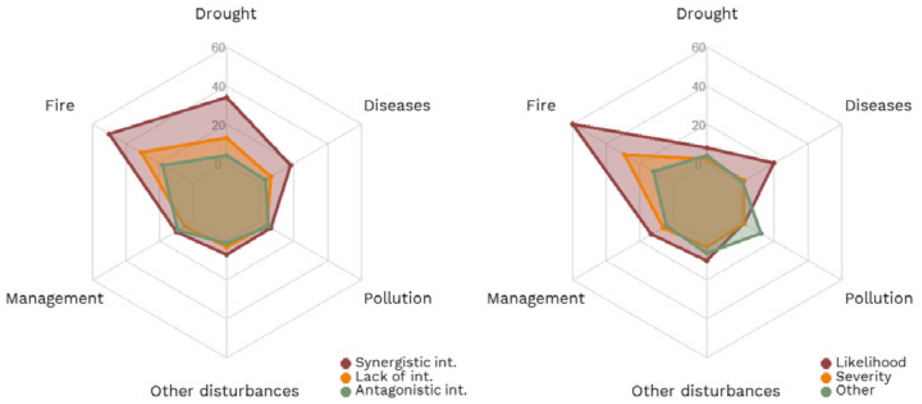
▶ FIGURE 1
Geographical distribution of number of studies at continental level. Solid filled circles indicate the distribution of the 216 papers addressing interactions between insect pests and other forest disturbances included in the review. Striped circles indicate the distribution of papers addressing forest disturbances.



▶ FIGURE 2
Proportion of studies addressing each insect species, grouped by insect feeding guild.

DISTURBANCE INTERACTIONS

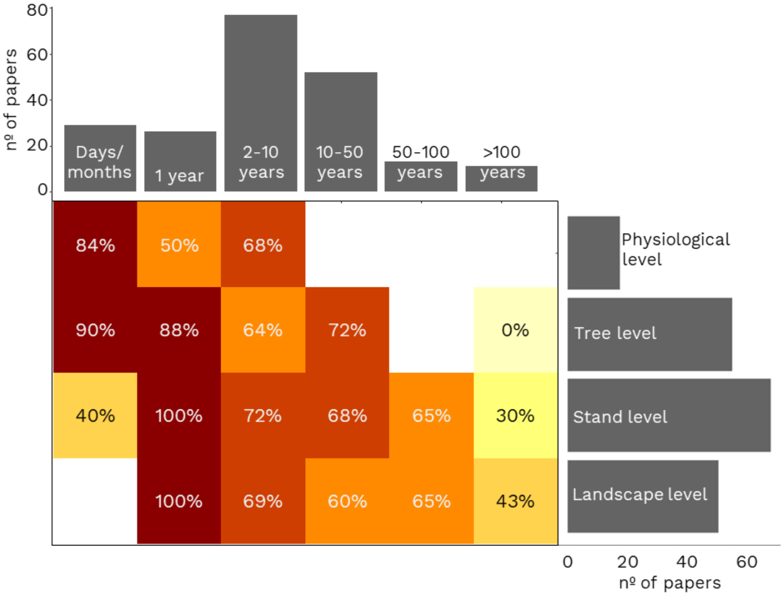
Interactions between fire and forest insect pests were the most commonly studied (41%; FIG. 3). Of these fire-insect studies, 48% examined how insect-induced tree mortality affects fuel loads and consequent fire activity, 36% investigated how fire promotes insect attacks, and 16% looked at how fire and insect pests together affect forest structure and composition. The second most studied interaction was with drought (24%). Such publications investigated how water-stressed trees are more susceptible to insect attacks and how insect outbreaks can increase the vulnerability of trees to moisture stress. Other interacting agents included forest diseases (11%), forest management (10%), pollution (6%), and wind and winter storm events (5%). Finally, 3% of studies examined other types of forest disturbances (e.g., landslides and floods). Although we did not explicitly include climate change as a disturbance in our list, it was considered in 48% of the papers examined.



▶ **FIGURE 3**
Number of papers reporting synergistic interactions, antagonistic interactions, and a lack of interactions between insect pest and each type of forest disturbance (left panel). Number of papers analyzing influences on the likelihood, severity, or another type of response between insect pests and each type of forest disturbance (right panel).

SPATIAL AND TEMPORAL SCALES

A similar number of studies focused on disturbance interactions at landscape scale (26%), stand scale (35%), and tree scale (30%), and only 9% of the studies focused on the physiological scale (FIG. 4). Simulation modeling studies tended to focus on landscapes (48%) and stands (44%) and much less on trees (8%; FIG. 5). Temporal scales covered a broad range, from a few days to hundreds of years, although most of the studies focused on interactions occurring between 2 and 9 years (36%) or 10 and 49 years (24%; FIG. 4). Longer temporal scales were more frequent in simulation model studies, where 10–49 years accounted for 60% of studies and 50–99 years 48% (FIG. 5).



▶ FIGURE 4
Histograms of spatial and temporal scales used by reviewed studies. Heatmap indicates the percentage of interactions or lack of the interaction reported.

IMPACT AND SOURCES OF VARIATION

Most studies reported the occurrence of interactions between disturbances (71%), considering both synergistic (54%) and antagonistic relationships (17%; FIG. 3). We found that interactions were more often identified at shorter time scales than at longer ones, while the interactions were more frequently identified at the physiological, tree, and stand scales (74%, 75%, and 71% respectively), than at landscape scale (65%; FIG. 4). However, logistic regressions showed that the presence of disturbance interactions was not significantly affected by spatial ($r^2 = 0.34$, p-value > 0.41) or temporal scales ($r^2 = 0.11$, p-value = 0.15). Similarly, relationships between temporal or spatial scales and the disturbance agent involved were not statistically significant ($r^2 = 0.18$, p-value > 0.06 and $r^2 = 0.14$, p-value > 0.13, respectively). However, interactions between fire and insect pests were identified more often at short, than at long temporal scales ($Z = |1.15|$, p-value = 0.06 and $Z = |1.03|$, p-value = 0.07 at temporal scale categories 1 year and 2-9 years, respectively).

No disturbance was found to play a role in interaction occurrence more frequently than any other ($r^2 = 0.11$, p-value > 0.12 in all levels). In terms of frequencies, insect pest and forest management interactions occurred in 79% of the reviewed papers; insects and diseases, 77%; insects and drought, 74%; insects and pollution, 73%; insects and wind, 67%; insects and fire, 67%; and the two studies addressing insect pests interacting with storms and landslides also reported interactions (FIG. 3). No insect feeding guild tended to be more associated with interaction occurrence than any other ($r^2 = 0.17$, p-value > 0.91 in all levels). We also found no significant association between the occurrence of an interaction and the order of occurrence of the disturbances ($r^2 = 0.14$, p-value = 0.31). Nonetheless, we found that insects tended to follow fires in 57% of the reviewed studies, whereas fire followed insect pest outbreaks in 76% of the studies. We also found that the interaction of drought followed by xylem/phloem feeder insect pests occurred significantly more often than other combinations ($Z = 48.79$, p-value < 0.001).

Studies varied in terms of the specific effects of disturbance interactions they examined. For example, most of the studies reviewed (59%) investigated how an initial disturbance influences the likelihood of a subsequent one and, of these studies, disturbance interactions were successfully identified in 73% of the cases (FIG. 3). Other papers (27%) examined how a disturbance affects the severity of subsequent disturbances, finding such an interaction in 70% of cases. Finally, some studies examined how multiple disturbances affect other features, like disturbance spread (10%) or competitiveness of insect pests (4%). However, logistic regressions showed that no interaction type was more associated with interaction occurrence than any other ($r^2 = 0.13$, p-value > 0.10 for any type), neither in the case of any disturbance agent in particular ($r^2 = 0.12$, p-value > 0.06).

SIMULATION MODELS AND INTERACTIONS BETWEEN DISTURBANCES

We found 23 articles (11%) that used simulation models to investigate the interaction between insect pests and other disturbances. Again, the most frequently studied interaction was between insect outbreaks and wildfires (82%), followed by interactions with drought (35%; FIG. 5). Nine articles included three forest disturbances in a model (insect pests plus two other disturbances; FIG. 5). Almost all the models operated at either the landscape or stand scale (96%), and the most common temporal scale was 10–49 years, although some made projections over as many as 300 years. Most of the studies (63%) used previously published models (e.g., LANDIS, SORTIE, LandClim) while some built and used their own models. Many models used forest attributes (e.g., individual tree diameter, age, basal area, tree species), disturbance severity (for both insect pests and the interacting disturbance), and climatic variables as inputs. Other variables such as topography, forest spatial distribution, and soil properties were only occasionally considered. Data sources were mainly external empirical data, either from public repositories or from published studies (70%). Only in eight articles did authors compile their own data and in one case model data were simulated. With respect to scenarios, most of the studies tested models under different scenarios, either simulating different disturbance intensities and/or the effects of different IPCC climate scenarios (83%; Moss et al. 2010). Finally, simulation-model studies reported finding interactions between disturbances at a similar frequency as the empirical studies reviewed here (68%).

▸ **FIGURE 5**
Studies assessing insect pest interactions with other disturbances via simulation models showing the disturbances included, the temporal and spatial scales used, and the explanatory variables considered. Table next page.

		Disturbance					Temporal scale						Spatial scale			Variables included						Data source			Scenarios		
Reference	Model	Fire	Drought	Diseases/Other pests	Management	Other disturbances	< 1 year	1 year	2-9 years	10-49 years	50-99 years	>100 years	Tree level	Stand level	Landscape level	Forest structure	Climate variables	Disturbance severity	Spatial disposition	Topography	Soil	External empirical data	Own empirical data	Simulated data	Single	Multiple climate scn.	Multiple dist. intensity scn.
Ager et al. 2007	*FVS-PPE, Westwide Pine Beetle M.*	▨			▨					▨	▨			▨		▨						▨					▨
Chapin et al. 1997	*Frame-based model*	▨										▨			▨		▨					▨				▨	
Chew et al. 2004	*SIMPPLLE*	▨		▨	▨			▨	▨						▨	▨		▨	▨			▨			▨		
Derose et al.2009	*FVS-FFE, Fire and Fuels Extension*	▨								▨	▨	▨		▨		▨						▨	▨				▨
Gustafson et al.2010	*LANDIS-II*	▨	▨		▨					▨	▨	▨			▨	▨	▨	▨		▨		▨				▨	
Hansen et al.2015	*FVS-FFE, Fire and Fuels Extension*	▨								▨				▨		▨	▨	▨		▨		▨	▨		▨		
Hoffman et al.2012a	*WFDS*	▨						▨	▨					▨		▨		▨		▨			▨		▨		
Hoffman et al.2012b	*WFDS*	▨					▨						▨	▨		▨		▨	▨	▨			▨				▨
James et al.2011	*VLM*	▨			▨				▨	▨	▨	▨			▨	▨		▨		▨	▨	▨					▨
Linn et al.2013	*HIGRAD/FIRETEC*	▨				▨	▨	▨						▨			▨	▨					▨				▨
Loehman et al.2017	*FireBGC*	▨	▨	▨						▨	▨	▨		▨		▨	▨	▨		▨		▨					▨
Lucash et al.2018	*LANDIS-II*	▨	▨		▨	▨				▨	▨				▨	▨	▨	▨		▨		▨				▨	
Maroschek et al.2015	*PICUS*		▨		▨	▨		▨	▨	▨					▨	▨	▨	▨		▨		▨				▨	▨
Nitschke et al.2012	*SORTIE*	▨	▨							▨	▨	▨		▨		▨	▨						▨			▨	
Økland et al. 2016	*Spread model*					▨			▨				▨			▨			▨				▨				▨
Potterf et al.2017	*IPS*					▨			▨						▨	▨			▨			▨					▨
Scheller et al.2018	*LANDIS-II*	▨	▨		▨					▨	▨	▨			▨	▨	▨	▨		▨	▨	▨				▨	▨
Seidl et al.2016	*FVS-FFE, Fire and Fuels Extension*	▨								▨	▨	▨		▨		▨		▨				▨			▨		
Sieg et al.2017	*HIGRAD/FIRETEC*	▨				▨		▨	▨					▨		▨		▨				▨					▨
Simard et al.2011	*Nexus*	▨						▨	▨	▨				▨		▨	▨	▨		▨	▨		▨				▨
Sturtevant et al.2012	*LANDIS-II*	▨								▨	▨	▨			▨	▨	▨	▨			▨	▨					▨
Temperli et al.2013	*LandClim*		▨		▨	▨				▨	▨				▨	▨	▨	▨			▨	▨				▨	▨
Temperli et al.2015	*LandClim*	▨	▨			▨				▨	▨				▨	▨	▨	▨			▨			▨		▨	

Discussion

Global change is increasing the frequency and severity of disturbances and the uncertainty linked to disturbance interactions. Understanding forest ecosystem dynamics in such a context requires integrated research approaches that consider both individual disturbances and their interactive effects. In surveying the published literature regarding the reciprocal influence of forest insect pests on other disturbances, we found that interactions with fire and drought were the most frequently studied. We found that any of the factors considered (i.e., disturbance agent, type of response, insect feeding guild, or spatial and temporal scale) could be associated with the probability of an interaction being detected and reported in the scientific literature. Finally, simulation models were used in only 23 publications despite their enormous potential to help us further unravel how complex interactions among climate change, forest disturbance, and forest recovery processes contribute to forest dynamics and ecosystem resilience.

GEOGRAPHIC COVERAGE AND BIAS

Most studies of interactions between insect pests and other disturbances were conducted in North America and Europe. However, these two continents also produced most of the published papers on forest disturbances in general, with or without interactions. There are likely two main reasons for this, acting in combination: first, the reported absolute forest area affected by disturbances is larger in North America (followed by Europe, Africa, and Asia, respectively) than on other continents (FAO 2008; Parker et al. 2006; Weed et al. 2013). Second, as a result of economic and educational factors, scientific research output in general tends to be higher in North America and Europe (Gonzalez-Brambila et al. 2016; Smith et al. 2014).

The insect species represented in our survey reflect the geographic distribution of these studies, thus most of the insect pests studied were from North America and Europe. The most common species were those that exhibit large-scale and periodic outbreaks, such as the mountain pine beetle (*Dendroctonus ponderosae*) and the eastern spruce budworm (*Choristoneura fumiferana*), as well as other Coleopteran phloem feeders such as the North American spruce beetle (*Dendroctonus rufipennis*) and the European spruce bark beetle (*I. typographus*). These species attract greater research attention as they have large impacts on forests around the globe in terms of extent and severity, and they commonly occur in regions that are also subject to fires, drought, and forest management (FAO 2008). The economic consequences of outbreaks of these species for management agencies and the forest industry are not negligible (Chang et al. 2012). However, our findings suggest that other insect pests in other regions are understudied, such as the brown Christmas beetle (*Anoplognathus chloropyrus*) and the eucalyptus weevil (*Gonipterus scutellatus*) that interact with fires in Australia (Carnegie et al. 2005; Loch and Matsuki 2010), and the dynamics of the latter (*G. scutellatus*) also being related to drought in South Africa (Graziosi et al. 2020).

FOREST DISTURBANCES INTERACTING WITH INSECT PESTS

Fire – insect pests

Fire is the most studied disturbance that interacts with insect pests (TABLE 2). Although there is a well-established hypothesis that insect attacks lead to the accumulation of more fuel and a consequent amplification of wildfire susceptibility (McCullough et al. 1998), the studies we reviewed provided mixed evidence of positive, negative, and no effect of insects on wildfire (James et al. 2017; Jenkins et al. 2014; Meigs et al. 2015; Parker et al. 2006) (FIG. 2). Studies showing evidence of insect-induced fire highlight the increase in litter (Agne et al. 2016; Jenkins 2011), crown fuel accumulation (Hoffman et al. 2012; Jolly et al. 2012; Simard et al. 2011; Woolley et al. 2019), vertical connectivity (Candau et al. 2018; Crotteau et al. 2018; Watt et al. 2018), flammability of needles (Jolly et al. 2012), and wind penetration due to the lack of leaves (Linn et al. 2013) as the main drivers of the interaction, leading to high risk of ignition, spread, and severity of fire (Bigler et al. 2005; Kulakowski and Thomas 2007). Other authors did not find a positive link between insect outbreaks and fire, arguing that insect attacks reduce forest fuel connectivity and therefore fire activity (DeRose and Long 2009). Still other studies have suggested that the varying responses of fire ignition to insect activity is due to the different temporal scales at which researchers have looked for these interactions: when examining the effect of spruce budworm (*C. fumiferana*) outbreaks on fire ignition risk in Ontario (Canada), James et al. (2017) found that immediately following an outbreak the risk decreased but, nine to ten years after the outbreak, ignition risk increased. However, at broad spatiotemporal scales, studies found that other factors such as climate, forest structure, and topography had a greater influence on fire ignition risk than did the spatial legacies of past insect outbreaks (Andrus et al. 2016; Speer and Kulakowski 2017). The specific ecology of the insect species of interest (Cohen et al. 2016; Meigs et al. 2015), severity of the outbreak (Meigs et al. 2015, 2016; Simard et al. 2011), and eco-regional context (James et al. 2017) also affect fire-insect relationships.

Fires also shape the probability of insect outbreaks, directly through their effects on tree resistance and indirectly through their effects on forest structure and succession. Interactions between fire and insects affect successional trajectories by reducing regeneration potential (Veblen et al. 2006). Alternatively, the compounded effects of fire and insects also facilitate regeneration by reducing tree competition, favoring seed dispersal (Land and Rieske 2006; Liang et al. 2016), changing forest-age structure (Arbellay et al. 2017), and replacing dominant species (Bergeron et al. 1993). A study on the spruce budworm (*C. fumiferana*) system suggests no effect of fire-insect interactions on long-term forest composition due to rapid regeneration of its primary host (Sturtevant et al. 2012).

In terms of direct effects, non-stand-replacing fires compromise tree defenses, making them more susceptible to insect attacks, due to both a reduction in bark thickness and to stress, which reduces resin production (Boulanger et al. 2013; Bradley and Tueller 2001; Davis et al. 2012; Lombardero and Ayres 2011; Ryan and Amman 1996; Santoro et al. 2001). Fire-injured trees also synthesize and accumulate ethanol, monoterpenes, and hormones that, once released to the atmosphere, act as primary attractant for some insect species such as *Dendroctonus valens*, *D. brevicomis*, *Gnathotrichus pilosus*, or *Hylurgops porosus* (Beh et al. 2014; Kelsey and Joseph 2003; Kelsey and Westlind 2017a; Westlind and Kelsey 2019), which can promote outbreaks.

Drought – insect pests

Much like fire-stress, drought influences insect-pest outbreaks because drought-stressed trees synthesize chemicals that act as insect attractants and, at the same time, may reduce their leaf- and stem-water potential limiting their resistance to insect attacks (Anderegg et al. 2015; Kelsey et al. 2014; Kelsey and Joseph 2001; Klutsch et al. 2017; Lusebrink et al. 2011). In the case of defoliators, drought stress can increase tree vulnerability as trees produce fewer palatable leaves and therefore insects need to consume more foliage to survive (Backhaus et al. 2014). Stressed trees are also limited in their ability to capture nutrients (McNulty and Boggs 2010) and produce resins, which makes them less able to defend themselves against insect attacks and therefore more vulnerable (Sangüesa-Barreda et al. 2015; Wong and Daniels 2017).

Conversely, insect outbreaks increase tree vulnerability to water stress. When trees are attacked by insects the crown and/or roots are damaged, compromising water-regulation capacity. Thus, trees become more susceptible to later episodes of extreme drought leading to higher mortality rates (Allen et al. 2010; Altmann 2013; Anderegg et al. 2015; DeRose and Long 2012; Kolb et al. 2016; McDowell et al. 2008; McDowell et al. 2010). Some authors have down-played the relevance of drought-insect interactions arguing that such interactions are secondary relative to other factors, such as tree fitness or the consequences of forest management (Hart et al. 2015). Indeed, some studies have proposed that water stress reduces trees' vulnerability to insect attack because of the less hospitable environment insects experience in a drought-stressed tree (Hart et al. 2014; Kolb et al. 2016). Yet other studies have provided evidence that defoliators can enhance tree water status by reducing canopy transpiration under drought, which is called the defoliation paradox (Bouzidi et al. 2019; Itter et al. 2019)

Diseases or other insect pests – insect pests

Insect pests also interact with other biotic disturbances, such as diseases, pathogens, and other insects. These interactions may take the form of mutualisms, such as in the case where insects act as vectors for fungal infections such as Dutch elm disease or beech bark disease (the first caused by fungus *Ophiostoma ulmi* and the second by *Neonectria faginata* and *N. ditissima;* Addison et al. 2014; Aukema et al. 2010; Ceriani-Nakamurakare et al. 2016; Firmino et al. 2017; Pinna et al. 2019; Rankin and Borden 1991; Reed et al. 2015; Shanahan et al. 2016; Xu et al. 2018) or vectors for other bark beetle species (Croise and Lieutier 1993). As happens in the cases of fire and drought, when insects or fungi attack trees, they induce the production of volatile chemicals that attract other insects (Aukema et al. 2006; Grégoire et al. 2015; Kelsey and Manter 2004; Martini et al. 2017). However, inter-specific competition among insects or pathogens may diminish effects on host trees (Kennedy and McCullough 2002; Kopper et al. 2004; Rankin and Borden 1991; Tabacaru and Erbilgin 2015).

Forest management – insect pests

Pest control through forest management is a major topic that is out of the scope of this review. However, forest management (whether focused on pest control or not) causes alterations to forest landscapes and may interact with insect pest disturbances. Forest management affects insect outbreaks both negatively and positively (FIG. 3) and at different scales, from individual trees to landscapes (Ager et al. 2007; Hindmarch and Reid 2001; Johansson et al. 2007; Temperli et al.

2014). Thinning, prescribed burning, and commercial plantations change forest composition, landscape mosaics, and tree-age distributions. The “silvicultural hypothesis” states that forest diversity can mitigate the effects of outbreaking insects (Jactel and Brockerhoff 2007; Miller and Rusnock 1993). This hypothesis is supported by repeated observations that more diverse forest stands comprising hardwood species tend to experience less damage than homogenous coniferous stands do (Campbell et al. 2008; Su et al. 1996). Further, in a recent long-term study, Robert et al. (2018) found that the legacy of forest management strategies helped to explain the frequency, intensity, and spatial synchrony of spruce budworm (*C. fumiferana*) outbreaks. Removing dead trees, replanting new tree species, or prescribed burns interfered with outbreak development and spread (D’Amato et al. 2011; Rossi et al. 2011). Also, thinned stands were less susceptible to bark beetle species attack, likely because the plumes of pheromone the insects use for communication could not reach their targets (Thistle 2005), and because vigor and resistance to insect attacks was improved in thinned trees (Anhold et al. 1996; Macquarrie and Cooke 2011).

Pollution – insect pests

Pollution also interacts with insect pest disturbances. Most research indicates that pollutants reduce host-tree quality as well as insect fitness, leading to a reduction in insect attacks. For instance, high ozone concentrations reduce insect fecundity and colonization rates. Increased CO_2 and heavy metal concentrations reduce growth, survival, development, and size of larvae and adults (Kopper and Lindroth 2003). Acid rain negatively affects insects directly by causing mortality, or indirectly by reducing host-plant quality (Butler and Trumble 2008; Kinney et al. 1997). However, some studies find little influence of pollution on insect performance or even a positive influence (Awmack et al. 2004). Some aphids and lepidopterans increase their growth rate and survival under high concentration of SO_2, NO_2, or O_3 (Butler and Trumble 2008). Elevated concentrations of CO_2 may play a role in insect interactions with pathogens (Roth et al. 1998; Roth and Lindroth 1994; Stiling et al. 1999) or insects’ natural enemies (Percy et al. 2002), although most common responses were negative or neutral. Some studies verified that under simulated acid rain conditions, insect attacks were more severe than in the control situation (Palokangas and Neuvonen 1995; Saikkonen et al. 1995).

Other disturbances – insect pests

Other disturbances such as storms, windthrow, snow avalanches, and landslides influence insect outbreaks and their effects on forests. Together, these agents build a complex picture of direct, indirect, bidirectional, and multidirectional interactions. Such disturbances may cause changes in forest structure, compromising later insect attacks (Hanewinkel et al. 2008; Louis et al. 2014; Perovich and Sibold 2016). Also, after severe gales, storms, or landslides, the accumulation of dead wood and hence the probability of insect attacks may increase (Howe and Baker 2003; Simard and Lajeunesse 2015; Yamazaki 2011). Finally, some authors have mentioned that episodes of strong winds might facilitate the spread of insect pests (Havašová et al. 2017; Potterf and Bone 2017; Stadelmann et al. 2014).

Climate change – insect pests

Climate change is not a forest disturbance in itself, but it has been widely recognized as a major driver of changes in insect pest regimes (Bolte et al. 2010; DeRose and Long 2012; Pawson et al. 2017; Rogers et al. 2017; Rouault et al. 2006; Temperli et al. 2015; Temperli et al. 2013). Like many of the disturbances we have discussed, climate change influences insect pests both directly and indirectly. In terms of direct effects, increases in temperature and changes in moisture availability may increase insect survival and development rates (van Lierop et al. 2015; Malesky et al. 2018). These changes are likely to lead to shifts in geographic distributions (Bolte et al. 2010; DeRose and Long 2012; Friedenberg et al. 2008; Jaime et al. 2019; Marini et al. 2017; Pawson et al. 2017; Renwick et al. 2016; Rogers et al. 2017; Schwartzberg et al. 2014), although such positive feedback is still under discussion (Pyšek et al. 2010). In terms of indirect effects, climate change affects insect pests through direct and indirect influence on other agents (Pechony and Shindell 2010; Seidl and Rammer 2017; Seidl et al. 2017; Temperli et al. 2013).

▶ **TABLE 2**
Summary of main perturbations interacting with insect pests, their interaction cause, and its ecological explanation.

DISTURBANCE	INTERACTION CAUSE	ECOLOGICAL EXPLANATION	REFERENCES
Fire	Fuel load and connectivity	Insect-caused tree mortality or reduction of biomass moisture content alter fuel amount and connectivity, as well as the likelihood of subsequent wildfire severity.	Andrus et al. 2016; Candau, Fleming, and Wang 2018; Chapin and Starfield 1997; Chen et al. 2017; Crotteau et al. 2018; DeRose and Long 2009; Donato et al. 2013; Flemin, Candau, and McAlpine 2002; Hansen et al. 2016; Hart, Schoennagel, et al. 2015; Harvey et al. 2013, 2014; Harvey, Donato, and Turner 2014; C. Hoffman et al. 2012; C. M. Hoffman et al. 2012; Hummel and Agee 2003; James et al. 2011a, 2017; Jenkins 2011; Jolly et al. 2012; Jorgensen and Jenkins 2010; Klutsch et al. 2011; Kulakowski and Jarvis 2011; Kulakowski and Thomas 2007; Liang et al. 2016; Linn et al. 2013; Lynch and Moorcroft 2008; Makoto et al. 2012; McCarley et al. 2017; Meigs et al. 2015, 2016; Mietkiewicz and Kulakowski 2016; Mietkiewicz, Kulakowski, and Veblen 2018; Navarro et al. 2018; W. G. Page and Jenkins 2007; W. Page and Jenkins 2007; Perrakis et al. 2014; Prichard and Kennedy 2014; Schoennagel et al. 2012; Sieg et al. 2017; Simard et al. 2011; Talucci and Krawchuk 2019; Watt et al. 2018; Woolley et al. 2019
	Attraction to the tree	Fire causes tree stress, leading to an increase of ethanol, monoterpenes and pheromones production that attract insects. Also, burned deadwood favors insect attacks.	Beh et al. 2014; Coleman et al. 2008; Kelsey and Joseph 2003; Kelsey and Westlind 2017a; Liang et al. 2016; Lombardero, Ayres, and Ayres 2006; Veblen et al. 2006; Westlind and Kelsey 2019
	Tree susceptibility to insects	Fire weakens the defensive system of the surviving trees in terms of resins and other metabolites contributing to insect pest establishment.	Amman and Ryan 1991; Bebi, Kulakowski, and Veblen 2003; Bradley and Tueller 2001; Chen-Charpentier and Leite 2014; Davis, Hood, and Bentz 2012; Ehnström, Långström, and Hellqvist 1995; Elkin and Reid 2004; Kulakowski and Jarvis 2013; Loehman et al. 2017; Lombardero and Ayres 2011; Lombardero, Ayres, and Ayres 2006; McNichol et al. 2019; Pohl, Hadley, and Arabas 2006; Powell, Townsend, and Raffa 2012; Ryan and Amman 1996; Santoro et al. 2001; Schwilk et al. 2006; Verble and Stephan 2009

DISTURBANCE	INTERACTION CAUSE	ECOLOGICAL EXPLANATION	REFERENCES
Fire	Forest structure and composition	A first disturbance (fire or insect pest) causes changes in forest structure (in terms of age, species, understory, etc.) and favors a second disturbance (pest or fire).	Bakaj et al. 2016; Bebi, Kulakowski, and Veblen 2003; Bergeron, Pierre-Rene, and Dansereau 1993; Bigler, Kulakowski, and Veblen 2005; Boucher et al. 2018; Boulanger, Sirois, and Hébert 2013; Coleman et al. 2008; C. Fettig, Borys, and Dabney 2010; Hanula et al. 2002; Johansson et al. 2007; Kerns and Westlind 2013; Kulakowski et al. 2012; Kulakowski, Veblen, and Beb 2016; Kulakowski, Veblen, and Bebi 2003; Lynch et al. 2006; Lynch and Moorcroft 2008; Menges and Deyrup 2001; O'Connor et al. 2015; Perovich and Sibold 2016; Seidl et al. 2016; Stevens-Rumann, Morgan, and Chad 2015
	Forest consequences	Coexistence of insect pest and fire compromises forest regeneration, that is species establishment and tree growth.	Burton and Boulanger 2018; C. J. Fettig et al. 2008; Harvey et al. 2013, 2014; Harvey, Donato, and Turner 2014; J. A. Hicke, Meddens, and Kolden 2015; Kulakowski et al. 2013; Land and Rieske 2006; Liang et al. 2016; Menges and Deyrup 2001; Stevens-Rumann, Morgan, and Chad 2015; Sturtevant et al. 2012; Vepakomma, Kneeshaw, and St-Onge 2010
Drought	Attraction to the tree	Drought causes tree stress, leading to an increase of ethanol, monoterpenes, sugars and pheromones production that attracts insects. New climatic conditions may alter leaf palatability or deadwood accumulation, compromising insect attraction.	Backhaus et al. 2014; Bolte et al. 2010; Caldeira et al. 2002; Castagneyrol, Moreira, and Jactel 2018; Haavik et al. 2015; Hale et al. 2005; Hart et al. 2014; Hogg, Brandt, and Kochtubajda 2002; Itter et al. 2019; Kelsey et al. 2014; Kelsey and Joseph 2001; Klutsch, Shamoun, and Erbilgin 2017; S. F. Ward et al. 2019
	Tree susceptibility to insect	Drought weakens the defensive system of trees (e.g., resins and other metabolites, water potential) and reduced capacity of fixing nitrogen which contributes to insect pest establishment.	Anderegg et al. 2015; Arango-Velez et al. 2014; Birch et al. 2019; Björkman 2000; Croise and Lieutier 1993; Dunn and Lorio 1993; Durand-Gillmann et al. 2014; Flake and Weisberg 2019; Flower et al. 2014; Gaylord et al. 2013; Jaime et al. 2019; Larsson and Björkman 1993; Lucash et al. 2018; McNulty and Boggs 2010; Moise, Lavigne, and Johns 2019; Negron et al. 2009; Pohl, Hadley, and Arabas 2006; Sangüesa-Barreda, Linares, and Camarero 2015; Scheller et al. 2018; Suárez-Vidal et al. 2019; Temperli et al. 2015; Wermelinger et al. 2008; Wong and Daniels 2017

	Tree susceptibility to drought	Insect pest attacks compromise tree response to later drought disturbances.	Altmann 2013; Bouzidi et al. 2019; Cailleret et al. 2017; DeRose and Long 2012; Itter et al. 2019; Lloret and Kitzberger 2018
	Forest structure and composition	Drought modifies forest structure and composition, directly kills trees and following insects cannot establish.	Hart, Veblen, et al. 2015
Diseases or other pests	Attraction to the tree	A first pest disturbance causes tree stress leading to an increase of ethanol, monoterpenes and pheromones production, which attracts a second pest disturbance.	Aukema et al. 2006; Beh et al. 2014; Gehring, Cobb, and Whitham 2013; Grégoire et al. 2015; Kelsey and Manter 2004; Kenaley, Mathiasen, and Harner 2008; Martini et al. 2017
	Insect vector and symbiosis	Insects and other pest have a direct or indirect symbiotic collaborative relationship that includes insects acting as vectors for other forest diseases, promoting their spread and establishment.	Addison et al. 2014; Aukema et al. 2010; Ceriani-Nakamurakare et al. 2016; Firmino et al. 2017; Pinna et al. 2019; Rankin and Borden 1991; Reed et al. 2015; Shanahan et al. 2016; Xu et al. 2018
	Interspecific competition	Insects compete for space, resources, or protect trees from second infestations.	Borkowski and Skrzecz 2016; Bylund and Tenow 1994; Jones, Hanlon, and Paine 2015; Kennedy and McCullough 2002; Kopper, Klepzig, and Raffa 2004; Maňák et al. 2013, 2015; Rankin and Borden 1991; C. A. Tabacaru and Erbilgin 2015; Crisia A. Tabacaru, McPike, and Erbilgin 2015

DISTURBANCE	INTERACTION CAUSE	ECOLOGICAL EXPLANATION	REFERENCES
Management	Forest consequences	Landscape pattern changes due the interaction of insect pests and forest management.	C. J. Fettig et al. 2008; Mladenoff, Boyce, and Radeloff 2000
	Attraction to the tree	Management causes tree stress leading to an increase of monoterpenes production what attracts insects.	Bauce and Fuentealba 2013; Leverkus et al. 2018
	Forest structure and composition	Forest management reduces insect pest attacks by changing tree species, structure, and density.	(Zhang et al. 1993; Anhold et al. 1996; Ager et al. 2007; Johansson et al. 2007; Hayes et al. 2008; Berthiaume et al. 2009; Fettig et al. 2010; Gustafson et al. 2010; Rossi et al. 2011, 2018; Schwab et al. 2011; D'Amato et al. 2011; James et al. 2011a; Temperli et al. 2014; Nowak et al. 2015; Rosenberger et al. 2017; Leite et al. 2018; Cotton-Gagnon et al. 2018; Restaino et al. 2019)
Pollution and acid rain	Tree susceptibility to insects	Host tree fitness affected by high CO_2, O_3, other pollutants, or acid rain may consequently alter later insect attacks.	Agrell et al. 2005; Awmack, Harrington, and Lindroth 2004; Coviella and Trumble 1999; Docherty et al. 1997; Holopainen et al. 1993; Holton, Lindroth, and Nordheim 2003; Kidd 1990; Kinney et al. 1997; Kozlov, Zverev, and Zvereva 2017; Lindroth, Kinney, and Platz 1993; McDonald, Agrell, and Lindroth 1999; S. Roth et al. 1998; S. K. Roth and Lindroth 1994; Williams, Lincoln, and Thomas 1994
	Natural enemies	Pollution demonstrates a disrupted synchrony between natural enemies and insects.	K. T. Saikkonen and Neuvonen 1993

Other disturbances	Forest structure and composition	Disturbances causes changes in forest structure and composition, compromising later insect attacks.	Hanewinkel et al. 2008; Radl, Lexer, and Vacik 2017; Crisia Alexandra Tabacaru, Park, and Erbilgin 2016; Thom et al. 2013
	Tree susceptibility to insects	Disturbances such snow, storms, wind, or floods weakens the defensive system of trees (e.g., resins and other metabolites) contributing to insect pest establishment	Angulo-Sandoval et al. 2004; Howe and Baker 2003; Hunter and Forkner 1999; Reyes and Kneeshaw 2008; Yoneya, Kugimiya, and Takabayashi 2014
	Insect dispersion	Wind favors insect dispersion	Havašová, Ferenčík, and Jakuš 2017; Potterf and Bone 2017
	Tree susceptibility to other disturbances	Insect pest compromises tree root systems exposing them to more susceptibility to debris slides.	Simard and Lajeunesse 2015

SOURCES OF VARIATION IN DISTURBANCE INTERACTIONS

The interactions between insect pests and other forest disturbances highlighted in this review were often significant and synergistic (FIG. 3). Disturbances disrupt the structure and composition of ecosystems, create heterogeneous landscape mosaics, and change the physical environment (White et al. 1985; Turner 2010). In doing so, they can force ecosystem renewal, cause temporal disorganization, and alter the susceptibility of forests to new disturbances. Such synergistic interactions are especially important for the dynamics of biotic disturbances in a changing climate (Seidl et al. 2017).

In this review, we aimed to identify the main elements that favor or limit forest disturbance interactions. Different authors emphasize the relevance of the particular insect species involved in the interaction (Hanula et al. 2002; Joseph et al. 2001; Kelsey and Westlind 2017a; Meigs et al. 2015, 2016), as different species tend to have different autecologies and vary in terms of feeding strategies, even within feeding guilds. Further, some species were studied more than others with respect to their interactions with other disturbances (e.g., the interactions between *Dendroctonus* spp. and *C. fumiferana* with fire). We therefore hypothesized that insect feeding guild (i.e., defoliators vs. xylem/phloem feeders) might be associated with particular disturbances, but the results presented here did not support this theory. Only disturbances caused by xylem/phloem feeders tended to occur more frequently following periods of drought, probably due to the higher concentration of soluble sugars in the bark of water-stressed trees resulting in improved insect larvae performance (Caldeira et al. 2002).

We hypothesized that interactions between disturbances might be more frequent at smaller spatial (at the physiological- and tree-scale) and temporal scales (one year or less; FIG. 4). When larger spatiotemporal scales are considered, there may be more agents and processes that influence forest dynamics and disturbance and, therefore, it becomes more difficult to identify clear relationships between disturbances. Also, interactions at small spatiotemporal scales, such as positive attraction of insects at the physiological scale a few days after a fire or drought, are probably unlikely to translate into landscape-scale outbreaks (Kelsey et al. 2016; Kelsey and Joseph 2001, 2003; Kelsey and Westlind 2017b, 2017a). However, although we identified differences in the frequency of interactions according to spatial and temporal scale, these were not significant. Thus, we concluded that scales are not correlated with the probability of identifying an interaction between two disturbances.

Studies of interactions between disturbances include a broad range of disturbance-specific features (e.g., fire disturbances are described with respect to size, severity, probability of ignition) that may affect the interaction. This is the case that Meigs (2015, 2016) and Harvey (2013, 2014) presented when they reported that insect attacks did not increase fire likelihood but altered its severity and spread. Thus, in this study we specified the type of response in disturbance interactions reported in every study (influences on the likelihood, severity, spread or insect fitness). Most of the reviewed papers that focused on insect-fire interactions examined how increased fuel loads caused by insect attacks (according to the duration of defoliation and time since the end of defoliation) facilitate subsequent fire ignition (e.g., Watt et al. 2020). In respect of severity, studies such as Derose and Long (2009) and Donato et al. (2013) reported a reduction in fire severity following insect attack because defoliation resulted in reduced horizontal and vertical fuel connectivity. However, our results showed that the occurrence of interactions between disturbances was not correlated with the type of response considered, either for the specific case of fire or for other disturbances. Only a small relationship between pollution and its impacts on insect fitness was found. Thus, we highlight the importance of characterizing the specific nature of disturbance interactions and the consequences on disturbed ecosystems, in addition to identifying when and where an interaction occurs.

THE ROLE OF SIMULATION MODELS

There is increasing interest in examining the combined effects of multiple disturbances on landscape dynamics (Chew et al. 2004; Lucash et al. 2018; Scheller et al. 2018; Seidl et al. 2016; Tabacaru et al. 2016; Temperli et al. 2015). However, empirical approaches are limited in their ability to address such complex questions because past disturbances may provide an insufficient basis to understand potential future changes resulting from climate change, invasive species, and increasing human activity (Temperli et al. 2015; Temperli et al. 2013). Simulation modeling provides one useful approach to studying future landscape changes and exploring emergent dynamics (Perera 2015).

Nonlinear, cross-scale interactions are inherent in forest landscape dynamics (e.g., interactions at tree level may leave a footprint at the landscape level; Peters et al. 2007). Empirical approaches have limited application at broad temporal and spatial scales or when processes occur across scales. Most of the modeling studies we reviewed used spatially explicit models at the scale of the landscape or stand.

These models also explored longer time frames than did empirical studies (FIG. 5), of up to 300 years (Hoffman et al. 2012; James et al. 2011a; Loehman et al. 2017; Sturtevant et al. 2012). The ability to explore long-term dynamics is essential in the case of insect pest disturbances because of the long term spatial legacies they can create and, in some cases, the cyclical population dynamics they generate (FIG. 5; Robert et al. 2020).

Future environmental change is uncertain, as are the dynamics of stochastic disturbances. Simulation models allows for the explicit integration of this uncertainty through scenario testing. Model-mediated exploration of such uncertain parameter space is essential to improve understanding of how different sources of uncertainty might impact the target system. Most of the articles we examined here engaged in some sort of scenario testing. (FIG. 5). Scenarios were mainly used to analyze the role of climate change in forest disturbances, usually using the IPCC climate projections (Moss et al. 2010). Other studies used scenarios to test different disturbance impacts or the response of the affected habitat (FIG. 5). Long-term projections based on a range of plausible scenarios are also valuable in facilitating policy development (Morán-Ordóñez et al. 2018; Økland et al. 2016).

While a modeling approach has benefits relative to relying on historical empirical data (e.g., the opportunity to observe unexpected emergent phenomena), developing spatial models of forest disturbance interactions can be challenging. A central challenge relates to the acquisition of high-quality data for parameterizing complex spatially-explicit simulation models, especially at large scales. Indeed, the lack of such information often stimulates the adoption of a modeling approach. Some authors collected their own data to calibrate the model (DeRose and Long 2009; Hansen et al. 2015; Hoffman et al. 2012; Hoffman et al. 2012; Linn et al. 2013; Nitschke et al. 2012; Økland et al. 2016; Simard et al. 2011), whereas others used another approach, simulating the input data of the model based on expert knowledge (Temperli et al. 2015). Most modeling studies we reviewed here used data from public repositories or from other publications (FIG. 5). Long-term data monitoring and remote sensing data are particularly useful in landscape dynamics modeling because these sources offer continuous information in time and/or space (Ager et al. 2007; Chapin and Starfield 1997; Gustafson et al. 2010).

Other challenges to developing useful models of forest disturbance include integrating multiple relevant processes and their interactions at different spatiotemporal scales, as well as modeling them in a mechanistic way (Baker and Robinson 2010). Addressing these challenges requires explicit assumptions and simplifications, compromising realism while maintaining coherence, internal consistency, and plausible descriptions of modelled dynamics (Baker and Robinson 2010; Morán-Ordóñez et al. 2018). Thus, when working with multiple disturbances, one is restricted to including only relevant landscape variables (one or a few in number) both as explanatory and response variables (e.g., stand volume, species; Clark and Gelfand 2006; Gustafson et al. 2010).

Of the 216 articles we reviewed, only 23 were based on simulation models. However, interest in using simulation modeling to explore disturbance interactions seems to be increasing: 83% of the model-based studies were published after 2010. Given the utility of simulation models mentioned above, both in scientific research and in the development of forest policies, we would emphasize the importance of the further development of simulation modeling capacity through research on how to better model complex processes and their multi-scale dynamics. To complement such model development, additional empirical information is required to improve model parameterization and model predictions, and it is the reciprocal interaction between empirical and simulation studies that will identify new challenges and opportunities and move our collective understanding forward.

EMERGING DISTURBANCES AND CHALLENGES TO THEIR STUDY

Climate change, increasing global trade, and land-use change all have the potential to alter interactions between insect pests and other disturbances. Such drivers lead to an increase in invasive species that will compromise host ecosystems (Brockerhoff et al. 2006; Choi et al. 2019; Dix and Britton 2014; van Lierop et al. 2015; Lovett et al. 2006; Smith et al. 2012; Ward and Masters 2007). Some species considered to be invasive were introduced centuries ago and their effects on ecosystems are usually considered alongside native species. That is the case with the gypsy moth (*L. dispar*), which is of Euro Asiatic origin but was introduced to the US at the end of the 19th century (Kinney et al. 1997; McDonald et al. 1999; Roth et al. 1998). However, impacts of recent invasive insect pests are hard to predict because there is little empirical evidence about their performance in new environments with new competitors. One such species is the box tree moth (*Cydalima perspectalis*) native to Asia, which has been invading European forests since 2007 (Bras et al. 2019). Its defoliating effect leads to the death of box trees (*Buxus sempervirens*), which are abundant in the understories of European forests. This may cause an increase in fuel availability and consequently affect the severity of fire risk or, conversely, it may reduce the probability of fire spread by eliminating the main understory species and reducing fuel connectivity.

Land-use change poses another challenge to understanding interactions between insects and other forest disturbances. It is broadly assumed that the replacement of primary forests with pastures and croplands causes a reduction in insect biodiversity, as seen in different ecosystems around the world (Almeida et al. 2011; Koh 2007; Korasaki et al. 2013; Meijer et al. 2011). Moreover, Barragán et al. (2011) documented a loss in beetle functional diversity (based on food relocation, body size, daily activity period, and food preferences) as a result of land-use changes in Mexico. However, the study of land-use effects on insect pests is mainly focused on agriculture (Kiritani 2007; van Lierop et al. 2015), and few studies investigate forest insects in the context of land-use change (Rosenberger et al. 2017). An example may be the pine processionary moth (*Thaumetopoea pityocampa*), whose growth is linked to habitat type (Torres-Muros et al. 2017). Given rural abandonment and pine reforestation in the natural range of this insect species (Cervera et al. 2019; Pausas et al. 2008), an increase in pine processionary moth pest risk is possible. Thus, researchers and managers should acknowledge that current dynamics and management policy effects extend beyond the short-term and local scale and should pay special attention not only to current forest pests but also to those that may have future impacts.

Finally, it is essential to improve theoretical knowledge of outbreaking insect species (genetics, population dynamics, species ecology, and distribution) to better understand the mechanisms behind interaction dynamics (Ayres and Lombardero 2000; Loehman et al. 2017; Xu et al. 2018). Other authors have highlighted problems with obtaining high-quality data for such studies, because long-term and broad-scale monitoring is needed (Aukema et al. 2010; Gustafson et al. 2010; Hanula et al. 2002). New technologies and platforms, such as data obtained using satellites or LiDAR, as well as improved demographic and population genetic data, represent enormous resources with which we can better parameterize spatially-explicit simulation models (Chou et al. 2010; Hollaus and Vreugdenhil 2019).

Conclusions

Our review summarizes the current understanding of interactions between insect pest outbreaks and other forest disturbances and highlights the complexity of these processes. Such interactions are critical drivers of landscape dynamics in many forested systems. Reported interactions between disturbances were synergistic, antagonistic, or not detected. They were detected at different spatial (from tree to landscape level) and temporal (from days to century) scales and included various types of interaction (influences on the likelihood, severity, spread or insect fitness). However, we found no clear relation between such disturbance features and the occurrence of interactions.

The impacts of insect pest outbreaks are expected to increase with intensifying global change. The fitness and distribution of insect species are strongly influenced by climate. Furthermore, insect pest outbreaks can interact with pollution and land-use changes, and invasions by insect species are increasing as a result of global trade. Understanding the potential for altered interactions between insect pests and other disturbances as well as the emergence of novel interactions are major challenges in forest dynamics research. In this context, simulation models and spatially explicit simulations of potential future global-change scenarios may play an important role in the management of disturbance interactions and landscape dynamics because they can incorporate multiple drivers that operate at broad spatiotemporal scales and can be used to project possible future scenarios. Such predictions of future ecosystem conditions must be supported by appropriate theoretical knowledge and must be relevant to decision-making processes.

References

Addison A, Powell JA, Bentz BJ, Six DL (2014) Integrating models to investigate critical phenological overlaps in complex ecological interactions: The mountain pine beetle-fungus symbiosis. *J Theor Biol* 368:55–66. https://doi.org/10.1016/j.jtbi.2014.12.011

Ager AA, McMahan A, Hayes JL, Smith EL (2007) Modeling the effects of thinning on bark beetle impacts and wildfire potential in the Blue Mountains of eastern Oregon. *Landsc Urban Plan* 80:301–311. https://doi.org/10.1016/j.landurbplan.2006.10.010

Agne MC, Beedlow PA, Shaw DC, et al (2018) Interactions of predominant insects and diseases with climate change in Douglas-fir forests of western Oregon and Washington, U.S.A. *For Ecol Manage* 409:317–332. https://doi.org/10.1016/j.foreco.2017.11.004

Agne MC, Woolley T, Fitzgerald S (2016) Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. *For Ecol Manage* 366:73–86. https://doi.org/10.1016/j.foreco.2016.02.004

Agrell J, Kopper B, McDonald EP, Lindroth RL (2005) CO_2 and O_3 effects on host plant preferences of the forest tent caterpillar (*Malacosoma disstria*). *Glob Chang Biol* 11:588–599. https://doi.org/10.1111/j.1365-2486.2005.00924.x

Allen CD, Macalady AK, Chenchouni H, et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manage* 259:660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Almeida S, Louzada J, Sperber C, Barlow J (2011) Subtle land-use change and tropical biodiversity: dung beetle communities in cerrado grasslands and exotic pastures. *Biotropica* 43:704–710. https://doi.org/10.1111/j.1744-7429.2011.00751.x

Altmann SH (2013) Crown condition, water availability, insect damage and landscape features: Are they important to the Chilean tree *Nothofagus glauca* (Nothofagaceae) in the context of climate change? *Aust J Bot* 61:394–403. https://doi.org/10.1071/BT13015

Amman, GD, Ryan KC. (1991). Insect infestation of fire-injured trees in the Greater Yellowstone Area (Vol. 398). US Department of Agriculture, Forest Service, Intermountain Research Station.

Anderegg WRL, Allen CD, Hicke JA, et al (2015) Tree mortality from drought , insects , and their interactions in a changing climate. *New Phytol* 208:674–683. https://doi.org/10.1111/nph.13477

Andrus RA, Veblen TT, Harvey BJ, Hart SJ (2016) Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado. *Ecol Appl* 26:700–711. https://doi.org/10.1890/15-1121/suppinfo

Angulo-Sandoval P, Fernández-Marín H, Zimmerman JK, Aide TM (2004) Changes in patterns of understory leaf phenology and herbivory following hurricane damage. *Biotropica* 36:60. https://doi.org/10.1646/03002

Anhold J. A, Jenkins MJ, Long JN (1996) Management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. *West. J. Appl. For*. 11:50–53

Arango-Velez A, Galindo González LM, Meents MJ, et al (2014) Influence of water deficit on the molecular responses of *Pinus contorta* x *Pinus banksiana* mature trees to infection by the mountain pine beetle fungal associate, Grosmannia clavigera. *Tree Physiol* 34:1220–1239. https://doi.org/10.1093/treephys/tpt101

Arbellay E, Daniels LD, Mansfield SD, Chang AS (2017) Cambial injury in lodgepole pine (*Pinus contorta*): Mountain pine beetle vs fire. *Tree Physiol* 37:1611–1621. https://doi.org/10.1093/treephys/tpx102

Aukema BH, Richards GR, Krauth SJ, Raffa KF (2006) Species assemblage arriving at and emerging from trees colonized by *Ips pini* in the Great Lakes Region: partitioning by time since colonization, season, and host species. *Ann Entomol Soc Am* 97:117–129. https://doi.org/10.1603/0013-8746(2004)097[0117:saaaae]2.0.co;2

Aukema BH, Zhu J, Møller J, et al (2010) Predisposition to bark beetle attack by root herbivores and associated pathogens: Roles in forest decline, gap formation, and persistence of endemic bark beetle populations. *For Ecol Manage* 259:374–382. https://doi.org/10.1016/j.foreco.2009.10.032

Awmack CS, Harrington R, Lindroth RL (2004) Aphid individual performance may not predict population responses to elevated CO_2 or O_3. *Glob Chang Biol* 10:1414–1423. https://doi.org/10.1111/j.1365-2486.2004.00800.x

Ayres MP, Lombardero M (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci Total Environ* 62:. https://doi.org/10.1016/S0048-9697(00)00528-3

Backhaus S, Wiehl D, Beierkuhnlein C, et al (2014) Warming and drought do not influence the palatability of *Quercus pubescens* Willd. leaves of four European provenances. *Arthropod Plant Interact* 8:329–337. https://doi.org/10.1007/s11829-014-9313-4

Bakaj F, Mietkiewicz N, Veblen TT, Kulakowski D (2016) The relative importance of tree and stand properties in susceptibility to spruce beetle outbreak in the mid-20th century. *Ecosphere* 7:1–17. https://doi.org/10.1002/ecs2.1485

Baker PJ, Robinson A (2010) Review and comparison of tree- and stand-based forest growth models for potential integration into EnSym. University of Melbourne: Victoria, Australia.

Barbet-Massin M, Rome Q, Villemant C, Courchamp F (2018) Can species distribution models really predict the expansion of invasive species? *PLoS One* 13:1–14. https://doi.org/10.1371/journal.pone.0193085

Barragán F, Moreno CE, Escobar F, et al (2011) Negative impacts of human land use on dung beetle functional diversity. *PLoS One* 6:. https://doi.org/10.1371/journal.pone.0017976

Bauce É, Fuentealba A (2013) Interactions between stand thinning, site quality and host tree species on spruce budworm biological performance and host tree resistance over a 6 year period after thinning. *For Ecol Manage* 304:212–223. https://doi.org/10.1016/j.foreco.2013.05.008

Bebi P, Kulakowski D, Veblen TT. (2003) Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology* 84:362–371. https://doi.org/https://doi.org/10.1890/0012-9658(2003)084

Beh MM, Metz MR, Seybold SJ, Rizzo DM (2014) The novel interaction between Phytophthora ramorum and wildfire elicits elevated ambrosia beetle landing rates on tanoak, Notholithocarpus densiflorus. *For Ecol Manage* 318:21–33. https://doi.org/10.1016/j.foreco.2014.01.007

Bergeron Y, Pierre-Rene D, Dansereau PRP-R (1993) Predicting the composition of Canadian southern boreal forest in different fire cycles. *J Veg Sci* 4:827–832. https://doi.org/10.2307/3235621

Berthiaume R, Bauce É, Hébert C, Brodeur J (2009) Host tree age as a selective pressure leading to local adaptation of a population of a polyphagous Lepidoptera in virgin boreal forest. *Bull Entomol Res* 99:493–501. https://doi.org/10.1017/S0007485308006536

Bigler C, Kulakowski D, Veblen TT (2005) Multiple disturbance interactions and drought influence fire severity in rocky mountain subalpine forests. *Ecology* 86:3018–3029. https://doi.org/10.1890/05-0011

Birch JD, Lutz JA, Hogg EH, et al (2019) Decline of an ecotone forest: 50 years of demography in the southern boreal forest. *Ecosphere* 10:. https://doi.org/10.1002/ecs2.2698

Björkman C (2000) Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. *Oecologia* 123:223–231. https://doi.org/10.1007/s004420051009

Bolte A, Hilbrig L, Grundmann B, et al (2010) Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce-beech forest. *Eur J For Res* 129:261–276. https://doi.org/10.1007/s10342-009-0323-1

Borkowski A, Skrzecz I (2016) Ecological segregation of bark beetle (Coleopter Curculionida Scolytinae) infested Scots pine. *Ecol Res* 31:135–144. https://doi.org/10.1007/s11284-015-1322-y

Boucher D, Boulanger Y, Aubin I, et al (2018) Current and projected cumulative impacts of fire, drought, and insects on timber volumes across Canada. *Ecol Appl* 28:1245–1259. https://doi.org/10.1002/eap.1724

Boulanger Y, Sirois L, Hébert C (2013) Distribution patterns of three long-horned beetles (Coleoptera: Cerambycidae) shortly after fire in boreal forest: adults colonizing stands versus progeny emerging from trees. *Environ Entomol* 42:17–28. https://doi.org/10.1603/en12003

Bouzidi HA, Balducci L, Mackay J, Deslauriers A (2019) Interactive effects of defoliation and water deficit on growth, water status, and mortality of black spruce (*Picea mariana* (Mill.) B.S.P.). *Ann For Sci* 76:. https://doi.org/10.1007/s13595-019-0809-z

Bradley T, Tueller P (2001) Effects of fire on bark beetle presence on jeffrey pine in the Lake Tahoe basin. *For Ecol Manage* 142:205–214. https://doi.org/10.1016/S0378-1127(00)00351-0

Bras A, Avtzis DN, Kenis M, et al (2019) A complex invasion story underlies the fast spread of the invasive box tree moth (*Cydalima perspectalis*) across Europe. *J Pest Sci* (2004) 92:1187–1202. https://doi.org/10.1007/s10340-019-01111-x
Brockerhoff EG, Liebhold AM, Jactel H (2006) The ecology of forest insect invasions and advances in their management. *Can J For Res* 36:263–268. https://doi.org/10.1139/x06-013
Buma B, Wessman CA (2011) Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2:1–13. https://doi.org/10.1890/ES11-00038.1
Burton PJ, Boulanger Y (2018) Characterizing combined fire and insect outbreak disturbance regimes in British Columbia, Canada. *Landsc Ecol* 33:1997–2011. https://doi.org/10.1007/s10980-018-0710-4
Butler CD, Trumble JT (2008) Effects of pollutants on bottom-up and top-down processes in insect-plant interactions. *Environ Pollut* 156:1–10. https://doi.org/10.1016/j.envpol.2007.12.026
Bylund H, Tenow O (1994) Long-term dynamics of leaf miners, *Eriocrania* spp., on mountain birch: alternate year fluctuations and interaction with *Epirrita autumnata*. *Ecol Entomol* 19:310–318. https://doi.org/10.1111/j.1365-2311.1994.tb00247.x
Cailleret M, Jansen S, Robert EMR, et al (2017) A synthesis of radial growth patterns preceding tree mortality. *Glob Chang Biol* 23:1675–1690. https://doi.org/10.1111/gcb.13535
Caldeira M da C, Fernandéz V, Tomé J, Pereira JS (2002) Positive effect of drought on longicorn borer larval survival and growth on eucalyptus trunks. *Ann For Sci* 59:99–106. https://doi.org/10.1051/forest
Campbell EM, MacLean DA, Bergeron Y (2008) The severity of budworm-caused growth reductions in balsam fir/spruce stands varies with the hardwood content of surrounding forest landscapes. *For Sci* 54:195–205. https://doi.org/10.1093/forestscience/54.2.195
Candau JN, Fleming RA, Wang X (2018) Ecoregional patterns of spruce budworm-wildfire interactions in central Canada's Forests. Forests 9:. https://doi.org/10.3390/f9030137
Carnegie AJ, Stone C, Lawson S, Matsuki M (2005) Can we grow certified eucalypt plantations in subtropical Australia? An insect pest management perspective. *New Zeal J For Sci* 35:223–245
Castagneyrol B, Moreira X, Jactel H (2018) Drought and plant neighbourhood interactively determine herbivore consumption and performance. *Sci Rep* 8:1–12. https://doi.org/10.1038/s41598-018-24299-x
Ceriani-Nakamurakare E, Slodowicz M, Gonzalez-Audino P, et al (2016) Mycobiota associated with the ambrosia beetle *Megaplatypus mutatus*: Threat to poplar plantations. *Forestry* 89:191–200. https://doi.org/10.1093/forestry/cpw001
Cervera T, Pino J, Marull J, et al (2019) Understanding the long-term dynamics of forest transition: From deforestation to afforestation in a Mediterranean landscape (Catalonia, 1868–2005). *Land use policy* 80:318–331. https://doi.org/10.1016/j.landusepol.2016.10.006
Chang WY, Lantz VA, Hennigar CR, Maclean DA (2012) Economic impacts of forest pests: A case study of spruce budworm outbreaks and control in New Brunswick, Canada. *Can J For Res* 42:490–505. https://doi.org/10.1139/X11-190
Chapin FS, Starfield AM (1997) Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Clim Change* 35:449–461. https://doi.org/10.1023/A:1005337705025
Chen-Charpentier B, Leite MCA (2014) A model for coupling fire and insect outbreak in forests. *Ecol Modell* 286:26–36. https://doi.org/10.1016/j.ecolmodel.2014.04.008
Chen G, He Y, De Santis A, et al (2017) Assessing the impact of emerging forest disease on wildfire using Landsat and KOMPSAT-2 data. *Remote Sens Environ* 195:218–229. https://doi.org/10.1016/j.rse.2017.04.005
Chew JD, Stalling C, Moeller K (2004) Integrating knowledge for simulating vegetation change at landscape scales. *West J Appl For* 19:102–108. https://doi.org/10.1093/wjaf/19.2.102
Choi W Il, Nam Y, Lee CY, et al (2019) Changes in major insect pests of Pine forests in Korea over the last 50 years. *Forests* 10:1–15. https://doi.org/10.3390/f10080692
Chou CY, Song B, Hedden RL, et al (2010) Three-dimensional landscape visualizations: New technique towards wildfire and forest bark beetle management. *Forests* 1:82–97. https://doi.org/10.3390/f1020082
Clark JS, Gelfand AE (2006) A future for models and data in environmental science. *Trends Ecol Evol* 21:375–380. https://doi.org/10.1016/j.tree.2006.03.016
Cohen WB, Yang Z, Stehman S V., et al (2016) Forest disturbance across the conterminous United States from 1985-2012: The emerging dominance of forest decline. *For Ecol Manage* 360:242–252. https://doi.org/10.1016/j.foreco.2015.10.042

Coleman TW, Meeker JR, Clarke SR, Rieske LK (2008) The suppression of *Dendroctonus frontalis* and subsequent wildfire have an impact on forest stand dynamics. *Appl Veg Sci* 11:231–242. https://doi.org/10.3170/2008-7-18362

Colgan LJ, Erbilgin N (2010) The ecological interaction of the mountain pine beetle and jack pine budworm in the boreal forest. *For Chron* 86:766–774. https://doi.org/10.5558/tfc86766-6

Cotton-Gagnon A, Simard M, De Grandpré L, Kneeshaw D (2018) Salvage logging during spruce budworm outbreaks increases defoliation of black spruce regeneration. *For Ecol Manage* 430:421–430. https://doi.org/10.1016/j.foreco.2018.08.011

Coviella CE, Trumble JT (1999) Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conserv Biol* 13:700–712. https://doi.org/10.1046/j.1523-1739.1999.98267.x

Croise L, Lieutier F (1993) Effects of drought on the induced defence reaction of Scots pine to bark beetle-associated fungi. *Ann des Sci For* 50:91–97. https://doi.org/10.1051/forest:19930107

Crotteau JS, Keyes CR, Hood SM, et al (2018) Fuel dynamics after a bark beetle outbreak impacts experimental fuel treatments. *Fire Ecol* 14:13. https://doi.org/10.1186/s42408-018-0016-6

Cullingham CI, Cooke JEK, Dang S, et al (2011) Mountain pine beetle host-range expansion threatens the boreal forest. *Mol Ecol* 20:2157–2171. https://doi.org/10.1111/j.1365-294X.2011.05086.x

D'Amato AW, Troumbly SJ, Saunders MR, et al (2011) Growth and survival of picea glauca following thinning of plantations affected by eastern Spruce budworm. *North J Appl For* 28:105–150. https://doi.org/10.1007/978-1-4613-3421-7_3

Dale VH, Joyce LA, McNulty S, et al (2001) Climate change and forest disturbances. *Bioscience* 51:723. https://doi.org/10.1641/0006-3568(2001)051[0723:ccafd]2.0.co;2

Davis RS, Hood S, Bentz BJ (2012) Fire-injured ponderosa pine provide a pulsed resource for bark beetles. *Can J For Res* 42:2022–2036. https://doi.org/10.1139/x2012-147

Day JK, Pérez DM (2013) Reducing uncertainty and risk through forest management planning in British Columbia. *For Ecol Manage* 300:117–124. https://doi.org/10.1016/j.foreco.2012.11.035

DeRose RJ, Long JN (2009) Wildfire and spruce beetle outbreak: Simulation of interacting disturbances in the central Rocky Mountains. *Écoscience* 16:28–38. https://doi.org/10.2980/16-1-3160

DeRose RJ, Long JN (2012) Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest. *Can J For Res* 42:1649–1660. https://doi.org/10.1139/x2012-102

Dix ME, Britton K (2014) A dynamic invasive species research vision: opportunities and priorities 2009-29. *Invasive Species Natl Res Oppor Priorities Strateg Manag Framew* 1–222

Docherty M, Wade FA, Hurst DK, et al (1997) Responses of tree sap-feeding herbivores to elevated CO_2. *Glob Chang Biol* 3:51–59. https://doi.org/10.1046/j.1365-2486.1997.00096.x

Donato DC, Harvey BJ, Romme WH, et al (2013) Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. *Ecol Appl* 23:3–20. https://doi.org/10.1890/12-0772.1

Duane A, Brotons L (2018) Synoptic weather conditions and changing fire regimes in a Mediterranean environment. *Agric For Meteorol* 253–254:190–202. https://doi.org/10.1016/j.agrformet.2018.02.014

Dunn JP, Lorio PL (1993) Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L to *Dendroctonus frontalis* (Coleoptera, Scolytidae). *Environ Entomol* 22:948–957. https://doi.org/10.1093/ee/22.5.948

Durand-Gillmann M, Cailleret M, Boivin T, et al (2014) Individual vulnerability factors of Silver fir (*Abies alba* Mill.) to parasitism by two contrasting biotic agents: Mistletoe (Viscum album L. ssp. Abietis) and bark beetles (Coleoptera: Curculionidae: Scolytinae) during a decline process. *Ann For Sci* 71:659–673. https://doi.org/10.1007/s13595-012-0251-y

Ehnström B, Långström B, Hellqvist C (1995) Insects in burned forests - forest protection and faunal conservation (preliminary results). *Entomol Fenn* 6:109–117. https://doi.org/10.33338/ef.83846

Elkin CM, Reid ML (2004) Attack and Reproductive Success of Mountain Pine Beetles (Coleoptera: Scolytidae) in Fire-Damaged Lodgepole Pines. *Environ Entomol* 33:1070–1080. https://doi.org/10.1603/0046-225x-33.4.1070

FAO (2008) Salud y vitalidad de los bosques. 69–88

Fettig C, Borys R, Dabney C (2010) Effects of fire and fire surrogate treatments on bark beetle-caused tree mortality in the Southern Cascades, California. *For Sci* 56:60–73. https://doi.org/10.1093/forestscience/56.1.60

Fettig CJ, Borys RR, McKelvey SR, Dabney CP (2008) Blacks Mountain Experimental Forest: Bark beetle responses to differences in forest structure and the application of prescribed fire in interior ponderosa pine. *Can J For Res* 38:924–935. https://doi.org/10.1139/X07-243

Firmino PN, Calvao T, Ayres MP, Pimentel CS (2017) *Monochamus galloprovincialis* and *Bursaphelenchus xylophilus* life history in an area severely affected by pine wilt disease: Implications for forest management. *For Ecol Manage* 389:105–115. https://doi.org/10.1016/j.foreco.2016.12.027
Flake SW, Weisberg PJ (2019) Fine-scale stand structure mediates drought-induced tree mortality in pinyon–juniper woodlands. *Ecol Appl* 29:1–13. https://doi.org/10.1002/eap.1831
Fleming RA, Candau J-N, McAlpine RS (2002) Landscape-scale analysis of interactions between insect defoliation and forest fire in Central Canada. *Clim Change* 55:251–272. https://doi.org/https://doi.org/10.1023/A:1020299422491
Flower A, Gavin DG, Heyerdahl EK, et al (2014) Drought-triggered western spruce budworm outbreaks in the interior Pacific Northwest: A multi-century dendrochronological record. *For Ecol Manage* 324:16–27. https://doi.org/10.1016/j.foreco.2014.03.042
Friedenberg N a., Sarkar S, Kouchoukos N, et al (2008) Temperature extremes, density dependence, and southern pine beetle (Coleoptera: Curculionidae) population dynamics in east Texas. *Environ Entomol* 37:650–659. https://doi.org/10.1093/ee/37.3.650
Gaylord ML, Kolb TE, Pockman WT, et al (2013) Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytol* 198:567–578. https://doi.org/10.1111/nph.12174
Gehring CA, Cobb NS, Whitham TG (2013) The university of Chicago three - way interactions among ectomycorrhizal mutualists , scale insects , and resistant and susceptible pinyon pines reviewed work (s): 149:824–841. https://doi.org/https://doi.org/10.1086/286026
Gitau CW, Bashford R, Carnegie AJ, Gurr GM (2013) A review of semiochemicals associated with bark beetle (Coleoptera: Curculionidae: Scolytinae) pests of coniferous trees: A focus on beetle interactions with other pests and their associates. *For Ecol Manage* 297:1–14. https://doi.org/10.1016/j.foreco.2013.02.019
Gonzalez-Brambila CN, Reyes-Gonzalez L, Veloso F, Perez-Angón MA (2016) The scientific impact of developing nations. PLoS One 11:. https://doi.org/10.1371/journal.pone.0151328
Graziosi I, Tembo M, Kuate J, Muchugi A (2020) Pests and diseases of trees in Africa: A growing continental emergency. Plants, People, Planet 2:14–28. https://doi.org/10.1002/ppp3.31
Grégoire DM, Quiring DT, Royer L, et al (2015) Indirect host-mediated effects of an exotic phloem-sap feeder on a native defoliator of balsam fir. For Ecol Manage 341:1–7. https://doi.org/10.1016/j.foreco.2015.01.001
Gustafson EJ, Shvidenko AZ, Sturtevant BR, Scheller RM (2010) Predicting global change effects on forest biomass and composition in south-central Siberia. *Ecol Appl* 20:700–715. https://doi.org/https://doi.org/10.1890/08-1693.1
Haavik LJ, Billings SA, Guldin JM, Stephen FM (2015) Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe. *For. Ecol. Manage.* 354:190–205
Hale BK, Herms DA, Hansen RC, et al (2005) Effects of drought stress and nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance of poplar to two lymantriid defoliators. *J Chem Ecol* 31:2601–2620. https://doi.org/10.1007/s10886-005-7616-8
Hanewinkel M, Breidenbach J, Neeff T, Kublin E (2008) Seventy-seven years of natural disturbances in a mountain forest area - the influence of storm, snow, and insect damage analysed with a long-term time series. *Can J For Res* 38:2249–2261. https://doi.org/10.1139/X08-070
Hansen EM, Johnson MC, Bentz BJ, et al (2015) Fuel loads and simulated fire behavior in "old-stage" beetle-infested ponderosa pine of the Colorado Plateau. *For Sci* 61:644–664. https://doi.org/10.5849/forsci.14-081
Hansen WD, Chapin FS, Naughton HT, et al (2016) Forest-landscape structure mediates effects of a spruce bark beetle (*Dendroctonus rufipennis*) outbreak on subsequent likelihood of burning in Alaskan boreal forest. *For Ecol Manage* 369:38–46. https://doi.org/10.1016/j.foreco.2016.03.036
Hanula JL, Meeker JR, Miller DR, Barnard EL (2002) Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida. *For Ecol Manage* 170:233–247. https://doi.org/10.1016/S0378-1127(01)00752-6
Hart SJ, Schoennagel T, Veblen TT, Chapman TB (2015a) Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proc Natl Acad Sci* 112:4375–4380. https://doi.org/10.1073/pnas.1424037112
Hart SJ, Veblen TT, Eisenhart KS, et al (2014a) Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* 95:930–939. https://doi.org/10.1890/13-0230.1

Hart SJ, Veblen TT, Kulakowski D (2014b) Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreaks in the early 21st century? *For Ecol Manage* 318:44–53. https://doi.org/10.1016/j.foreco.2013.12.035

Hart SJ, Veblen TT, Mietkiewicz N, Kulakowski D (2015b) Negative feedbacks on bark beetle outbreaks: Widespread and severe spruce beetle infestation restricts subsequent infestation. *PLoS One* 10:1–17. https://doi.org/10.1371/journal.pone.0127975

Harvey BJ, Donato DC, Romme WH, Turner MG (2014a) Fire severity and tree regeneration following bark beetle outbreaks: yhe role of outbreak stage and burning conditions. *Ecol Appl* 24:1608–1625. https://doi.org/10.1890/13-1851.1

Harvey BJ, Donato DC, Romme WH, Turner MG (2013) Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. *Ecology* 94:2475–2486. https://doi.org/https://doi.org/10.1890/13-0188.1

Harvey BJ, Donato DC, Turner MG (2014b) Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. *Proc Natl Acad Sci* 111:15120–15125. https://doi.org/10.1073/pnas.1411346111

Havašová M, Ferenčík J, Jakuš R (2017) Interactions between windthrow, bark beetles and forest management in the Tatra national parks. *For Ecol Manage* 391:349–361. https://doi.org/10.1016/j.foreco.2017.01.009

Hayes CJ, DeGomez TE, McMillin JD, et al (2008) Factors influencing pine engraver (*Ips pini* Say) colonization of ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) slash in Northern Arizona. *For Ecol Manage* 255:3541–3548. https://doi.org/10.1016/j.foreco.2008.02.037

Hessburg PF, Churchill DJ, Larson AJ, et al (2015) Restoring fire-prone Inland Pacific landscapes: seven core principles. *Landsc Ecol* 30:1805–1835. https://doi.org/10.1007/s10980-015-0218-0

Hicke J a., Johnson MC, Hayes JL, Preisler HK (2012) Effects of bark beetle-caused tree mortality on wildfire. *For Ecol Manage* 271:81–90. https://doi.org/10.1016/j.foreco.2012.02.005

Hicke JA, Meddens AJH, Kolden CA (2015) Recent tree mortality in the Western United States from bark beetles and forest fires. *For Sci* 62:141–153. https://doi.org/10.5849/forsci.15-086

Hindmarch TD, Reid ML (2001) Thinning of mature lodgepole pine stands increases scolytid bark beetle abundance and diversity. *Can J For Res* 31:1502–1512. https://doi.org/10.1139/cjfr-31-9-1502

Hoffman C, Parsons R, Morgan P, Mell R (2012a) Numerical simulation of crown fire hazard following bark beetle-caused mortality in lodgepole pine forests. *For Sci* 58:

Hoffman CM, Morgan P, Mell W, et al (2012b) Surface fire intensity influences simulated crown fire behavior in lodgepole pine forests with recent mountain pine beetle-caused tree mortality. *For Sci* 59:390–399. https://doi.org/10.5849/forsci.11-114

Hogg EH, Brandt JP, Kochtubajda B (2002) Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Can J For Res* 32:823–832. https://doi.org/10.1139/x01-152

Hollaus M, Vreugdenhil M (2019) Radar satellite imagery for detecting bark beetle outbreaks in forests. *Curr For Reports* 5:240–250. https://doi.org/10.1007/s40725-019-00098-z

Holopainen JK, Mustaniemi A, Kainulainen P, et al (1993) Conifer aphids in an air-polluted environment. I. Aphid density, growth and accumulation of sulphur and nitrogen by scots pine and Norway spruce seedlings. *Environ Pollut* 80:185–191. https://doi.org/10.1016/0269-7491(93)90146-F

Holton MK, Lindroth RL, Nordheim E V. (2003) Foliar quality influences tree-herbivore-parasitoid interactions: Effects of elevated CO_2, O_3, and plant genotype. *Oecologia* 137:233–244. https://doi.org/10.1007/s00442-003-1351-z

Howe E, Baker WL (2003) Landscape heterogeneity and disturbance interactions in a subalpine watershed in Northern Colorador, USA. *Ann Assoc Am Geogr* 93:797–813. https://doi.org/https://doi.org/10.1111/j.1467-8306.2003.09304002.x

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *J Appl Ecol* 46:10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Hummel S, Agee JK (2003) Western spruce budworm defoliation effects on forest structure and potential fire behavior. *Northwest Sci* 77:159–170

Hunter MD, Forkner RE (1999) Hurricane damage influences foliar polyphenolics and subsequent herbivory on surviving trees. *Ecology* 80:2676–2682. https://doi.org/10.1890/0012-9658(1999)080[2676:HDIFPA]2.0.CO;2

Itter MS, D'Orangeville L, Dawson A, et al (2019) Boreal tree growth exhibits decadal-scale ecological memory to drought and insect defoliation, but no negative response to their interaction. *J Ecol* 107:1288–1301. https://doi.org/10.1111/1365-2745.13087

Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecol Lett* 10:835–848. https://doi.org/10.1111/j.1461-0248.2007.01073.x

Jaime L, Batllori E, Margalef-Marrase J, et al (2019) Scots pine (*Pinus sylvestris* L.) mortality is explained by the climatic suitability of both host tree and bark beetle populations. *For Ecol Manage* 448:119–129. https://doi.org/10.1016/j.foreco.2019.05.070

James PMA, Fortin MJ, Sturtevant BR, et al (2011) Modelling Spatial Interactions Among Fire, Spruce Budworm, and Logging in the Boreal Forest. *Ecosystems* 14:60–75. https://doi.org/10.1007/s10021-010-9395-5

James PMA, Robert LE, Wotton BM, et al (2017) Lagged cumulative spruce budworm defoliation affects the risk of fire ignition in Ontario, Canada: *Ecol Appl* 27:532–544. https://doi.org/10.1002/eap.1463

Jenkins, M. J. (2011). Fuel and fire behavior in high-elevation five-needle pines affected by mountain pine beetle. In *In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 190-197.* (Vol. 63, pp. 190-197).

Jenkins MJ, Runyon JB, Fettig CJ, et al (2014) Interactions among the mountain pine beetle, fires, and fuels. *For Sci* 60:489–501

Johansson T, Hjältén J, Gibb H, et al (2007) Variable response of different functional groups of saproxylic beetles to substrate manipulation and forest management: Implications for conservation strategies. *For Ecol Manage* 242:496–510. https://doi.org/10.1016/j.foreco.2007.01.062

Jolly WM, Parsons R a., Hadlow AM, et al (2012) Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. *For Ecol Manage* 269:52–59. https://doi.org/10.1016/j.foreco.2011.12.022

Jones ME, Hanlon CC, Paine TD (2015) Potential for interspecific competition between congeneric longhorned beetle species (Coleoptera: Cerambycidae) in an adventive environment. *Environ Entomol* 44:960–965. https://doi.org/10.1093/ee/nvv070

Jorgensen CA, Jenkins MJ (2010) Fuel complex alterations associated with spruce beetle-induced tree mortality in intermountain spruce-fir forests, USA. *For Sci* 56:In pres: https://doi.org/https://doi.org/10.1093/forestscience/57.3.232

Joseph G, Kelsey RG, Peck RW, Niwa CG (2001) Response of some scolytids and their predators to ethanol and 4-allylanisole in pine forests of central oregon. *J Chem Ecol* 27:697–715. https://doi.org/10.1023/A:1010345817756

Keane RE, McKenzie D, Falk DA, et al (2015) Representing climate, disturbance, and vegetation interactions in landscape models. *Ecol Modell* 309–310:33–47. https://doi.org/10.1016/j.ecolmodel.2015.04.009

Kelsey RG, Gallego D, Sánchez-García FJ, Pajares J a. (2014) Ethanol accumulation during severe drought may signal tree vulnerability to detection and attack by bark beetles. *Can J For Res* 44:554–561. https://doi.org/10.1139/cjfr-2013-0428

Kelsey RG, Joseph G (2001) Attraction of scolytus unispinosus bark beetles to ethanol in water-stressed douglas-fir branches. *For Ecol Manage* 144:229–238. https://doi.org/10.1016/S0378-1127(00)00387-X

Kelsey RG, Joseph G (2003) Ethanol in ponderosa pine as an indicator of physiological injury from fire and its relationship to secondary beetles. *Can J For Res* 33:870–884. https://doi.org/10.1139/x03-007

Kelsey RG, Joseph G, Westlind D, Thies WG (2016) Ethanol and acetone from Douglas-fir roots stressed by Phellinus sulphurascens infection: Implications for detecting diseased trees and for beetle host selection. *For Ecol Manage* 360:261–272. https://doi.org/10.1016/j.foreco.2015.10.039

Kelsey RG, Manter DK (2004) Effect of Swiss needle cast on Douglas-fir stem ethanol and monoterpene concentrations, oleoresin flow, and host selection by the Douglas-fir beetle. *For Ecol Manage* 190:241–253. https://doi.org/10.1016/j.foreco.2003.10.019

Kelsey RG, Westlind DJ (2017a) Ethanol and primary attraction of red turpentine beetle in fire stressed ponderosa pine. *For Ecol Manage* 396:44–54. https://doi.org/10.1016/j.foreco.2017.04.009

Kelsey RG, Westlind DJ (2017b) Physiological stress and ethanol accumulation in tree stems and woody tissues at sublethal temperatures from fire. *Bioscience* 67:443–451. https://doi.org/10.1093/biosci/bix037

Kenaley S, Mathiasen R, Harner EJ (2008) Mortality associated with a bark beetle outbreak in dwarf mistletoe-infested ponderosa pine stands in Arizona. *West J Appl For* 23:113–120. https://doi.org/10.1093/wjaf/23.2.113

Kennedy A a., McCullough DG (2002) Phenology of the larger european pine shoot beetle *Tomicus piniperda* (L.) (Coleoptera: Scolytidae) in relation to native bark beetles and natural enemies in pine stands. *Environ Entomol* 31:261–272. https://doi.org/10.1603/0046-225x-31.2.261

Kerns BK, Westlind DJ (2013) Effect of season and interval of prescribed burn on ponderosa pine butterfly defoliation patterns. *Can J For Res* 43:979–983. https://doi.org/10.1139/cjfr-2013-0153

Kidd NAC (1990) The effects of simulated acid mist on the growth rates of conifer aphids and the implications for tree health. *J Appl Entomol* 110:524–529. https://doi.org/10.1111/j.1439-0418.1990.tb00152.x

Kingsolver JG, Arthur Woods H, Buckley LB, et al (2011) Complex life cycles and the responses of insects to climate change. *Integr Comp Biol* 51:719–732. https://doi.org/10.1093/icb/icr015

Kinney KK, Lindroth RL, Jung SM, Nordheim E V. (1997) Effects of CO_2 and NO_3-availability on deciduous trees: Phytochemistry and insect performance. *Ecology* 78:215–230. https://doi.org/10.2307/2265991

Kiritani K (2007) The impact of global warming and land-use change on the pest status of rice and fruit bugs (Heteroptera) in Japan. *Glob Chang Biol* 13:1586–1595. https://doi.org/10.1111/j.1365-2486.2007.01397.x

Klutsch JG, Battaglia MA, West DR, et al (2011) Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. *West J Appl For* 26:101–109. https://doi.org/10.1093/wjaf/26.3.101

Klutsch JG, Shamoun SF, Erbilgin N (2017) Drought stress leads to systemic induced susceptibility to a nectrotrophic fungus associated with mountain pine beetle in *Pinus banksiana* seedlings. *PLoS One* 12:. https://doi.org/10.7939/DVN

Koh LP (2007) Impacts of land use change on South-east Asian forest butterflies: A review. *J Appl Ecol* 44:703–713. https://doi.org/10.1111/j.1365-2664.2007.01324.x

Kolb TE, Fettig CJ, Ayres MP, et al (2016) Observed and anticipated impacts of drought on forest insects and diseases in the United States. *For Ecol Manage* 380:321–334. https://doi.org/10.1016/j.foreco.2016.04.051

Kopper BJ, Klepzig KD, Raffa KF (2004) Components of antagonism and mutualism in *Ips pini* – fungal interactions: Relationship to a life history of colonizing highly stressed and dead trees. *Environ Entomol* 33:28–34. https://doi.org/10.1603/0046-225x-33.1.28

Kopper BJ, Lindroth RL (2003) Responses of trembling aspen (*Populus tremuloides*) phytochemistry and aspen blotch leafminer (Phyllonorycter tremuloidiella) performance to elevated levels of atmospheric CO_2 and O_3. *Agric For Entomol* 5:17–26. https://doi.org/https://doi.org/10.1046/j.1461-9563.2003.00158.x

Korasaki V, Braga RF, Zanetti R, et al (2013) Conservation value of alternative land-use systems for dung beetles in Amazon: Valuing traditional farming practices. *Biodivers Conserv* 22:1485–1499. https://doi.org/10.1007/s10531-013-0487-3

Kozlov M V., Zverev V, Zvereva EL (2017) Combined effects of environmental disturbance and climate warming on insect herbivory in mountain birch in subarctic forests: Results of 26-year monitoring. *Sci Total Environ* 601–602:802–811. https://doi.org/10.1016/j.scitotenv.2017.05.230

Kulakowski D, Jarvis D (2011) The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: A look at the past century. *For Ecol Manage* 262:1686–1696. https://doi.org/10.1016/j.foreco.2011.07.016

Kulakowski D, Jarvis D (2013) Low-severity fires increase susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. *For Ecol Manage* 289:544–550. https://doi.org/10.1016/j.foreco.2012.10.020

Kulakowski D, Jarvis D, Veblen TT, Smith J (2012) Stand-replacing fires reduce susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. *J Biogeogr* 39:2052–2060. https://doi.org/10.1111/j.1365-2699.2012.02748.x

Kulakowski D, Matthews C, Jarvis D, Veblen TT (2013) Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*). *J Veg Sci* 24:168–176. https://doi.org/10.1111/j.1654-1103.2012.01437.x

Kulakowski D, Veblen TT (2007) Effect of prior disturbances on the extent and severeity of wildfire in colorado subalpine forests. *Ecology* 88:759–769. https://doi.org/https://doi.org/10.1890/06-0124

Kulakowski D, Veblen TT, Beb P (2016) Fire severity controlled susceptibility to a 1940s spruce beetle outbreak in Colorado, USA. *PLoS One* 11:1–16. https://doi.org/10.1371/journal.pone.0158138

Kulakowski D, Veblen TT, Bebi P (2003) Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *J Biogeogr* 30:1445–1456. https://doi.org/10.1046/j.1365-2699.2003.00912.x

Labandeira CC (2013) Deep-time patterns of tissue consumption by terrestrial arthropod herbivores. *Naturwissenschaften* 100:355–364. https://doi.org/10.1007/s00114-013-1035-4

Land AD, Rieske LK (2006) Interactions among prescribed fire, herbivore pressure and shortleaf pine (*Pinus echinata*) regeneration following southern pine beetle (*Dendroctonus frontalis*) mortality. *For Ecol Manage* 235:260–269. https://doi.org/10.1016/j.foreco.2006.08.336

Larsson S, Björkman C (1993) Performance of chewing and phloem-feeding insects on stressed trees. *Scand J For Res* 8:550–559. https://doi.org/10.1080/02827589309382801

Leite MCA, Chen-Charpentier B, Agusto FB (2018) Maximizing tree harvesting benefit from forests under insect infestation disturbances, *PloS ONE* 13:1-32. http://dx.doi.org/10.1371/journal.pone.0200575

Leverkus AB, Lindenmayer DB, Thorn S, Gustafsson L (2018) Salvage logging in the world's forests: Interactions between natural disturbance and logging need recognition. *Glob Ecol Biogeogr* 27:1140–1154. https://doi.org/10.1111/geb.12772

Liang L, Hawbaker TJ, Zhu Z, et al (2016) Forest disturbance interactions and successional pathways in the Southern Rocky Mountains. *For Ecol Manage* 375:35–45. https://doi.org/10.1016/j.foreco.2016.05.010

Lindroth RL, Kinney KK, Platz CL (1993) Responses of deciduous trees to elevated atmospheric CO_2: productivity, phytochemistry, and insect performance. *Ecology* 74:763–777. https://doi.org/10.2307/1940804

Linn RR, Sieg CH, Hoffman CM, et al (2013) Modeling wind fields and fire propagation following bark beetle outbreaks in spatially-heterogeneous pinyon-juniper woodland fuel complexes. *Agric For Meteorol* 173:139–153. https://doi.org/10.1016/j.agrformet.2012.11.007

Lloret F, Kitzberger T (2018) Historical and event-based bioclimatic suitability predicts regional forest vulnerability to compound effects of severe drought and bark beetle infestation. *Glob Chang Biol* 24:1952–1964. https://doi.org/10.1111/gcb.14039

Loch AD, Matsuki M (2010) Effects of defoliation by Eucalyptus weevil, Gonipterus scutellatus, and chrysomelid beetles on growth of Eucalyptus globulus in southwestern Australia. *For Ecol Manage* 260:1324–1332. https://doi.org/10.1016/j.foreco.2010.07.025

Loehman RA, Keane RE, Holsinger LM, Wu Z (2017) Interactions of landscape disturbances and climate change dictate ecological pattern and process: spatial modeling of wildfire, insect, and disease dynamics under future climates. *Landsc Ecol* 32:1447–1459. https://doi.org/10.1007/s10980-016-0414-6

Lombardero MJ, Ayres MP (2011) Factors influencing bark beetle outbreaks after forest fires on the Iberian Peninsula. *Environ Entomol* 40:1007–1018. https://doi.org/10.1603/en11022

Lombardero MJ, Ayres MP, Ayres BD (2006) Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens. *For Ecol Manage* 225:349–358. https://doi.org/10.1016/j.foreco.2006.01.010

Louis M, Grégoire JC, Pélisson PF (2014) Exploiting fugitive resources: How long-lived is "fugitive"? Fallen trees are a long-lasting reward for *Ips typographus* (Coleoptera, Curculionidae, Scolytinae). *For Ecol Manage* 331:129–134. https://doi.org/10.1016/j.foreco.2014.08.009

Lovett GM, Canham CD, Arthur MA, et al (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience* 56:395. https://doi.org/10.1641/0006-3568(2006)056[0395:fertep]2.0.co;2

Lucash MS, Scheller RM, Sturtevant BR, et al (2018) More than the sum of its parts: how disturbance interactions shape forest dynamics under climate change. *Ecosphere* 9:. https://doi.org/10.1002/ecs2.2293

Lusebrink I, Evenden ML, Blanchet FG, et al (2011) Effect of water stress and fungal inoculation on monoterpene emission from an historical and a new pine host of the mountain pine beetle. *J Chem Ecol* 37:1013–1026. https://doi.org/10.1007/s10886-011-0008-3

Lynch HJ, Moorcroft PR (2008) A spatiotemporal Ripley's *K* -function to analyze interactions between spruce budworm and fire in British Columbia, Canada. *Can J For Res* 38:3112–3119. https://doi.org/10.1139/X08-143

Lynch HJ, Renkin RA, Crabtree RL, Moorcroft PR (2006) The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 yellowstone fires. *Ecosystems* 9:1318–1327. https://doi.org/10.1007/s10021-006-0173-3

Macquarrie CJK, Cooke BJ (2011) Density-dependent population dynamics of mountain pine beetle in thinned and unthinned stands. *Can J For Res*. https://doi.org/10.1139/x11-007

Maino JL, Kong JD, Hoffmann AA, et al (2016) Mechanistic models for predicting insect responses to climate change. *Curr Opin Insect Sci* 17:81–86. https://doi.org/10.1016/j.cois.2016.07.006

Makoto K, Kamata N, Kamibayashi N, et al (2012) Bark-beetle-attacked trees produced more charcoal than unattacked trees during a forest fire on the Kenai Peninsula, Southern Alaska. *Scand J For Res* 27:30–35. https://doi.org/10.1080/02827581.2011.619566

Malesky DM, Bentz BJ, Brown GR, et al (2018) Effects of climate change on ecological disturbances. In: Climate Change Vulnerability and Adaptation in the Intermountain Region: Part II. US Department of Agriculture, Forest Service, Gen. Tech. Rep. RMRS-GTR-375. Fort Collins, CO, pp 199–263

Maňák V, Björklund N, Lenoir L, Nordlander G (2015) The effect of red wood ant abundance on feeding damage by the pine weevil Hylobius abietis. *Agric For Entomol* 17:57–63. https://doi.org/10.1111/afe.12080

Maňák V, Nordenhem H, Björklund N, et al (2013) Ants protect conifer seedlings from feeding damage by the pine weevil Hylobius abietis. *Agric For Entomol* 15:98–105. https://doi.org/10.1111/j.1461-9563.2012.00597.x

Marini L, Økland B, Jönsson AM, et al (2017) Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography* (Cop) 40:1426–1435. https://doi.org/10.1111/ecog.02769

Maroschek M, Rammer W, Lexer MJ (2015) Using a novel assessment framework to evaluate protective functions and timber production in Austrian mountain forests under climate change. *Reg Environ Chang* 15:1543–1555. https://doi.org/10.1007/s10113-014-0691-z

Martini X, Hughes MA, Killiny N, et al (2017) The fungus Raffaelea lauricola modifies behavior of its symbiont and vector, the redbay ambrosia beetle (*Xyleborus glabratus*), by altering host plant volatile production. *J Chem Ecol* 43:519–531. https://doi.org/10.1007/s10886-017-0843-y

McCarley TR, Kolden CA, Vaillant NM, et al (2017) Landscape-scale quantification of fire-induced change in canopy cover following mountain pine beetle outbreak and timber harvest. *For Ecol Manage* 391:164–175. https://doi.org/10.1016/j.foreco.2017.02.015

McCullough DG, Werner RA, Neumann D (1998) Fire and insects in northern and boreal forest ecosystems of North America. *Annu Rev Entomol* 43:107–127. https://doi.org/10.1146/annurev.ento.43.1.107

McDonald EP, Agrell J, Lindroth RL (1999) CO_2 and light effects on deciduous trees: Growth, foliar chemistry, and insect performance. *Oecologia* 119:389–399. https://doi.org/10.1007/PL00008822

McDowell N, Pockman WT, Allen CD, et al (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178:. https://doi.org/10.1111/j.1469-8137.2008.02436.x

McDowell NG, Allen CD, Marshall L (2010) Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational transect. *Glob Chang Biol* 16:399–415. https://doi.org/10.1111/j.1365-2486.2009.01994.x

McNichol BH, Montes CR, Barnes BF, et al (2019) Interactions between southern *Ips bark* beetle outbreaks, prescribed fire, and loblolly pine (*Pinus taeda* L.) mortality. *For Ecol Manage* 446:164–174. https://doi.org/10.1016/j.foreco.2019.05.036

McNulty SG, Boggs JL (2010) A conceptual framework: Redefining forest soil's critical acid loads under a changing climate. *Environ Pollut 1*58:2053–2058. https://doi.org/10.1016/j.envpol.2009.11.028

Meigs GW, Campbell JL, Zald HSJ, et al (2015) Does wildfire likelihood increase following insect outbreaks in conifer forests? *Ecosphere* 6:art118. https://doi.org/10.1890/ES15-00037.1

Meigs GW, Zald HSJ, Campbell JL, et al (2016) Do insect outbreaks reduce the severity of subsequent forest fires? *Environ Res Lett* 11:. https://doi.org/10.1088/1748-9326/11/4/045008

Meijer SS, Whittaker RJ, Borges PAV (2011) The effects of land-use change on arthropod richness and abundance on Santa Maria Island (Azores): Unmanaged plantations favour endemic beetles. J *Insect Conserv* 15:505–522. https://doi.org/10.1007/s10841-010-9330-2

Menges ES, Deyrup MA (2001) Postfire survival in south Florida slash pine: Interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. *Int J Wildl Fire* 10:53–63. https://doi.org/10.1071/WF01009

Mietkiewicz N, Kulakowski D (2016) Relative importance of climate and mountain pine beetle outbreaks on the occurrence of large wildfires in the western USA. *Ecol Appl* 26:2523–2535. https://doi.org/10.1002/eap.1400

Mietkiewicz N, Kulakowski D, Veblen TT (2018) Pre-outbreak forest conditions mediate the effects of spruce beetle outbreaks on fuels in subalpine forests of Colorado. *Ecol Appl* 28:457–472. https://doi.org/10.1002/eap.1661

Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. *Science* (80-) 349:

Miller A, Rusnock P (1993) The rise and fall of the silvicultural hypothesis in spruce budworm (*Choristoneura fumiferana*) management in eastern Canada. *For Ecol Manage* 61:171–189. https://doi.org/10.1016/0378-1127(93)90197-U

Moise ERD, Lavigne MB, Johns RC (2019) Density has more influence than drought on spruce budworm (*Choristoneura fumiferana*) performance under outbreak conditions. *For Ecol Manage* 433:170–175. https://doi.org/10.1016/j.foreco.2018.10.031

Morán-Ordóñez A, Roces-Díaz J V., Otsu K, et al (2018) The use of scenarios and models to evaluate the future of nature values and ecosystem services in Mediterranean forests. *Reg Environ Chang* 1–14. https://doi.org/10.1007/s10113-018-1408-5

Moss RH, Edmonds JA, Hibbard KA, et al (2010) The next generation of scenarios for climate change research and assessment. *Nature* 463:747–756. https://doi.org/10.1038/nature08823

Navarro L, Harvey AE, Ali A, et al (2018) A Holocene landscape dynamic multiproxy reconstruction: How do interactions between fire and insect outbreaks shape an ecosystem over long time scales? *PLoS One* 13:1–16. https://doi.org/10.1371/journal.pone.0204316

Negron, J. F., McMillin, J. D., Anhold, J. A., & Coulson, D. (2009). Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. *Forest Ecology and Management*, *257*(4), 1353-1362. https://doi.org/10.1016/j.foreco.2008.12.002

Nitschke CR, Amoroso M, Coates KD, Astrup R (2012) The influence of climate change, site type, and disturbance on stand dynamics in northwest British Columbia, Canada. *Ecosphere* 3:art11. https://doi.org/10.1890/ES11-00282.1

Nowak JT, Meeker JR, Coyle DR, et al (2015) Southern pine beetle infestations in relation to forest stand conditions, previous thinning, and prescribed burning: Evaluation of the southern pine beetle prevention program. *J For* 113:454–462. https://doi.org/10.5849/jof.15-002

O'Connor CD, Lynch AM, Falk DA, Swetnam TW (2015) Post-fire forest dynamics and climate variability affect spatial and temporal properties of spruce beetle outbreaks on a Sky Island mountain range. *For Ecol Manage* 336:148–162. https://doi.org/10.1016/j.foreco.2014.10.021

Økland B, Nikolov C, Krokene P, Vakula J (2016) Transition from windfall- to patch-driven outbreak dynamics of the spruce bark beetle *Ips typographus*. *For Ecol Manage* 363:63–73. https://doi.org/10.1016/j.foreco.2015.12.007

Page W, Jenkins MJ (2007a) Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. *For Sci* 53:662–674. https://doi.org/https://doi.org/10.1093/forestscience/53.6.662

Page WG, Jenkins MJ (2007b) Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. *For Sci* 53:507–518. https://doi.org/https://doi.org/10.1093/forestscience/53.4.507

Palokangas P, Neuvonen S (1995) The effects of simulated acid rain on growth and susceptibility to predation Phratora polaris (Col., Chrysomelidae). *Environ Pollut* 89:67–71. https://doi.org/https://doi.org/10.1016/0269-7491(94)00043-D

Parker TJ, Clancy KM, Mathiasen RL (2006) Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agric For Entomol* 8:167–189. https://doi.org/10.1111/j.1461-9563.2006.00305.x

Pausas JG, Llovet J, Anselm R, Vallejo R (2008) Are wildfires a disaster in the Mediterranean basin ? – A review Vegetation changes Shrublands dominated by resprouting species. *Int J Wildl Fire* 17:713–723. https://doi.org/10.1071/WF07151

Pawson SM, Marcot BG, Woodberry OG (2017) Predicting forest insect flight activity: A Bayesian network approach. *PLoS One* 12:1–23. https://doi.org/10.1371/journal.pone.0183464

Pechony O, Shindell DT (2010) Driving forces of global wildfires over the past millennium and the forthcoming century. *Proc Natl Acad Sci* 107:19167–19170. https://doi.org/10.1073/pnas.1003669107

Percy K, Awmack C, Lindroth R, et al (2002) Altered performance of forest pests under atmospheres enriched by CO_2 and O_3. *Nature* 420:403–408. https://doi.org/10.1038/nature01229.1.

Perera AH, Sturtevant BR, Buse LJ (2015) Simulation modeling of forest landscape disturbances: An overview. In *Simulation Modeling of Forest Landscape Disturbances* (pp. 1-15). Springer, Cham.

Perovich C, Sibold JS (2016) Forest composition change after a mountain pine beetle outbreak, Rocky Mountain National Park, CO, USA. *For Ecol Manage* 366:184–192. https://doi.org/10.1016/j.foreco.2016.02.010

Perrakis DDB, Lanoville R a., Taylor SW, Hicks D (2014) Modeling wildfire spread in mountain pine beetle-affected forest stands, British Columbia, Canada. *Fire Ecol* 10:10–35. https://doi.org/10.4996/fireecology.1002010

Peters DPC, Bestelmeyer BT, Turner MG (2007) Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. *Ecosystems* 10:790–796. https://doi.org/10.1007/s10021-007-9055-6

Pinna C, Linaldeddu BT, Deiana V, et al (2019) Plant pathogenic fungi associated with Coraebus florentinus (Coleoptera: Buprestidae) attacks in declining oak forests. *Forests* 10:. https://doi.org/10.3390/f10060488

Pohl K a., Hadley KS, Arabas KB (2006) Decoupling tree-ring signatures of climate variation, fire, and insect outbreaks in Central Oregon. *Tree-Ring Res* 62:37–50. https://doi.org/10.3959/1536-1098-62.2.37

Potterf M, Bone C (2017) Simulating bark beetle population dynamics in response to windthrow events. *Ecol Complex* 32:21–30. https://doi.org/10.1016/j.ecocom.2017.08.003

Powell EN, Townsend PA, Raffa KF (2012) Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. *Ecol Monogr* 82:69–84. https://doi.org/https://doi.org/10.1890/11-0607.1

Prichard SJ, Kennedy MC (2014) Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. *Ecol Appl* 24:571–590. https://doi.org/10.1890/13-0343.1

Pyšek P, Jarošík V, Hulme PE, et al (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proc Natl Acad Sci U S A* 107:12157–12162. https://doi.org/10.1073/pnas.1002314107

Radeloff VC, Mladenoff DJ, Boyce MS (2000) Effects of interacting disturbances on landscape patterns: Budworm defoliation and salvage logging. *Ecol Appl* 10:233–247. https://doi.org/https://doi.org/10.1890/1051-0761(2000)010[0233:EOIDOL]2.0.CO;2

Radl A, Lexer MJ, Vacik H (2017) A bayesian belief network approach to predict damages caused by disturbance agents. *Forests* 9:. https://doi.org/10.3390/f9010015

Raffa KF, Aukema BH, Bentz BJ, et al (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* 58:501–517. https://doi.org/10.1641/B580607

Rankin LJ, Borden JH (1991) Competitive interaction between the mountain pine beetle and the pine engraver in lodgepole. *Can J For Res* 21:1029–1036. https://doi.org/https://doi.org/10.1139/x91-141

Reed SE, Juzwik J, English JT, Ginzel MD (2015) Colonization of artificially stressed black walnut trees by ambrosia beetle, bark beetle, and other weevil species (Coleoptera: Curculionidae) in Indiana and Missouri. *Environ Entomol* 44:1455–1464. https://doi.org/10.1093/ee/nvv126

Renwick KM, Rocca ME, Stohlgren TJ (2016) Biotic disturbance facilitates range shift at the trailing but not the leading edge of lodgepole pine's altitudinal distribution. *J Veg Sci* 27:780–788. https://doi.org/10.1111/jvs.12410

Restaino C, Young DJN, Estes B, et al (2019) Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. *Ecol Appl* 29:1–14. https://doi.org/10.1002/eap.1902

Reyes GP, Kneeshaw D (2008) Moderate-severity disturbance dynamics in *Abies balsamea*-Betula spp. forests: The relative importance of disturbance type and local stand and site characteristics on woody vegetation response . *Écoscience* 15:241–249. https://doi.org/10.2980/15-2-3082

Robert LE, Sturtevant BR, Cooke BJ, et al (2018) Landscape host abundance and configuration regulate periodic outbreak behavior in spruce budworm *Choristoneura fumiferana*. *Ecography* (Cop) 41:1556–1571. https://doi.org/10.1111/ecog.03553

Robert LE, Sturtevant BR, Kneeshaw D, et al (2020) Forest landscape structure influences the cyclic-eruptive spatial dynamics of forest tent caterpillar outbreaks. *Ecosphere* 11:. https://doi.org/10.1002/ecs2.3096

Rogers BM, Jantz P, Goetz SJ (2017) Vulnerability of eastern US tree species to climate change. *Glob Chang Biol* 23:3302–3320. https://doi.org/10.1111/gcb.13585

Rosenberger DW, Venette RC, Aukema BH (2017) Development of an aggressive bark beetle on novel hosts: Implications for outbreaks in an invaded range. *J Appl Ecol* 55:1526–1537. https://doi.org/10.1111/1365-2664.13064

Rossi FJ, Carter DR, Alavalapati JRR, Nowak JT (2011) Assessing landowner preferences for forest management practices to prevent the southern pine beetle: An attribute-based choice experiment approach. *For Policy Econ* 13:234–241. https://doi.org/10.1016/j.forpol.2011.01.001

Rossi S, Plourde P-Y, Krause C (2018) Does a spruce budworm outbreak affect the growth response of black spruce to a subsequent thinning? *Front Plant Sci* 9:1–8. https://doi.org/10.3389/fpls.2018.01061

Roth S, Lindroth RL, Volin JC, Kruger EL (1998) Enriched atmospheric CO_2 and defoliation : effects on. *Glob Chang Biol* 419–430. https://doi.org/https://doi.org/10.1046/j.1365-2486.1998.00164.x

Roth SK, Lindroth RL (1994) Effects of CO_2-mediated changes in paper birch and white pine chemistry on gypsy moth performance. *Oecologia* 98:133–138. https://doi.org/10.1007/BF00341464

Rouault G, Candau J-N, Lieutier F, et al (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Ann For Sci* 63:613–624. https://doi.org/10.1051/forest:2006044

Ryan KC, Amman GD (1996) Bark beetle activity and delayed tree mortality in the greater Yellowstone area following the 1988 Fires. Ecol Implic fire Gt Yellowstone Proceedings Int Assoc Wildliand Fire, Fairland, WA 151–158

Saikkonen K, Neuvonen S, Kainulainen P (1995) Oviposition and larval performance of European pine sawfly in relation to irrigation, simulated acid rain and resin acid concentration in Scots pine. *Oikos* 74:273–282. https://doi.org/https://doi.org/10.2307/3545657

Saikkonen KT, Neuvonen S (1993) Effects of larval age and prolonged simulated acid rain on the susceptibility of European pine sawfly to virus infection. *Oecologia* 95:134–139. https://doi.org/10.1007/BF00649516

Sangüesa-Barreda G, Linares JC, Camarero JJ (2015) Reduced growth sensitivity to climate in bark-beetle infested Aleppo pines: Connecting climatic and biotic drivers of forest dieback. *For Ecol Manage* 357:126–137. https://doi.org/10.1016/j.foreco.2015.08.017

Santoro AE, Lombardero MJ, Ayres MP, Ruel JJ (2001) Interactions between fire and bark beetles in an old growth pine forest. *For Ecol Manage* 144:245–254. https://doi.org/10.1016/S0378-1127(00)00389-3

Scheller RM, Kretchun AM, Loudermilk EL, et al (2018) Interactions among fuel management, species composition, bark beetles, and climate change and the potential effects on forests of the lake Tahoe basin. *Ecosystems* 21:643–656. https://doi.org/10.1007/s10021-017-0175-3

Schoennagel T, Veblen TT, Negron JF, Smith JM (2012) Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. *PLoS One* 7:. https://doi.org/10.1371/journal.pone.0030002

Schwab O, Maness T, Bull G, et al (2011) Modeling the timber supply impact of introducing weevil-resistant spruce in British Columbia with cellular automata. *For Policy Econ* 13:61–68. https://doi.org/10.1016/j.forpol.2010.08.004

Schwartzberg EG, Jamieson MA, Raffa KF, et al (2014) Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia* 175:1041–1049. https://doi.org/10.1007/s00442-014-2960-4

Schwilk DW, Knapp EE, Ferrenberg SM, et al (2006) Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. *For Ecol Manage* 232:36–45. https://doi.org/10.1016/j.foreco.2006.05.036

Seidl R, Donato DC, Raffa KF, Turner MG (2016) Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. *Proc Natl Acad Sci* 113:13075–13080. https://doi.org/10.1073/pnas.1615263113

Seidl R, Rammer W (2017) Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. *Landsc Ecol* 32:1485–1498. https://doi.org/10.1007/s10980-016-0396-4

Seidl R, Schelhaas MJ, Lexer MJ (2011) Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Glob Chang Biol* 17:2842–2852. https://doi.org/10.1111/j.1365-2486.2011.02452.x

Seidl R, Thom D, Kautz M, et al (2017) Forest disturbances under climate change. *Nat Clim Chang* 7:395–402. https://doi.org/10.1038/nclimate3303

Shanahan E, Irvine KM, Thoma D, et al (2016) Whitebark pine mortality related to white pine blister rust, mountain pine beetle outbreak, and water availability. *Ecosphere* 7:. https://doi.org/https://doi.org/10.1002/ecs2.1610

Sieg CH, Linn RR, Pimont F, et al (2017) Fires following bark beetles: Factors controlling severity and disturbance interactions in ponderosa pine. *Fire Ecol* 13:1–23. https://doi.org/10.4996/fireecology.130300123

Simard M, Lajeunesse P (2015) The Interaction Between Insect Outbreaks and Debris Slides in a Glacial Valley of the Eastern Canadian Shield. *Ecosystems* 18:1281–1289. https://doi.org/10.1007/s10021-015-9897-2

Simard M, Romme WH, Griffin JM, Turner MG (2011) Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecol Monogr* 81:3–24. https://doi.org/10.1890/10-1176.1

Smith AL, Hewitt N, Klenk N, et al (2012) Effects of climate change on the distribution of invasive alien species in Canada: A knowledge synthesis of range change projections in a warming world. *Environ Rev* 20:1–16. https://doi.org/10.1139/a11-020

Smith MJ, Weinberger C, Bruna EM, Allesina S (2014) The scientific impact of nations: Journal placement and citation performance. *PLoS One* 9:1–6. https://doi.org/10.1371/journal.pone.0109195

Speer JH, Kulakowski D (2017) Creating a buzz: insect outbreaks and disturbance interactions. *Dendroecology*, 231–255. https://doi.org/10.4135/9781446247501.n1010

Stadelmann G, Bugmann H, Wermelinger B, Bigler C (2014) Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. *For Ecol Manage* 318:167–174. https://doi.org/10.1016/j.foreco.2014.01.022

Stevens-Rumann C, Morgan P, Chad H (2015) Bark beetles and wildfires: How does forest recovery change with repeated disturbances in mixed conifer forests? *Ecosphere* 6:art100. https://doi.org/10.1890/ES14-00443.1

Stiling P, Rossy AM, Hungate B, et al (1999) Decreased leaf-miner abundance in elevated CO_2: reduced leaf quality and increased parasitoid attack. *Ecol Appl* 9:240–244. https://doi.org/https://doi.org/10.1890/1051-0761(1999)009[0240:DLMAIE]2.0.CO;2

Sturtevant BR, Miranda BR, Shinneman DJ, et al (2012) Comparing modern and presettlement forest dynamics of a subboreal wilderness : Does spruce budworm enhance fire risk ? *Ecol Appl* 22:1278–1296. https://doi.org/https://doi.org/10.1890/11-0590.1

Su Q, NacLean DA., Needham TD (1996) The influence of hardwood content on balsam fir defoliation by spruce budworm. *Can J For Res* 26:1620–1628

Suárez-Vidal E, Sampedro L, Voltas J, et al (2019) Drought stress modifies early effective resistance and induced chemical defences of Aleppo pine against a chewing insect herbivore. *Environ Exp Bot* 162:550–559. https://doi.org/10.1016/j.envexpbot.2019.04.002

Tabacaru CA, Erbilgin N (2015) Competitors and natural enemies may cumulatively mediate *Dendroctonus ponderosae* colonization of burned Pinus forests. *For Ecol Manage* 337:98–109. https://doi.org/10.1016/j.foreco.2014.10.026

Tabacaru CA, McPike SM, Erbilgin N (2015) Fire-mediated interactions between a tree-killing bark beetle and its competitors. *For Ecol Manage* 356:262–272. https://doi.org/10.1016/j.foreco.2015.07.006

Tabacaru CA, Park J, Erbilgin N (2016) Prescribed fire does not promote outbreaks of a primary bark beetle at low-density populations. *J Appl Ecol* 53:222–232. https://doi.org/10.1111/1365-2664.12546

Talucci AC, Krawchuk M a. (2019) Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. *Ecosphere* 10:e02744. https://doi.org/10.1002/ecs2.2744

Taylor AR, Chen HYH, VanDamme L (2009) A review of forest succession models and their suitability for forest management planning. *For Sci* 55:23–36. https://doi.org/10.17221/73/2008-jfs

Temperli C, Bugmann H, Elkin C (2013) Cross-scale interactions among bark beetles, climate change, and wind disturbances: A landscape modeling approach. *Ecol Monogr* 83:383–402. https://doi.org/10.1890/12-1503.1

Temperli C, Hart SJ, Veblen TT, et al (2014) Are density reduction treatments effective at managing for resistance or resilience to spruce beetle disturbance in the southern Rocky Mountains? *For Ecol Manage* 334:53–63. https://doi.org/10.1016/j.foreco.2014.08.028

Temperli C, Veblen TT, Hart SJ, et al (2015) Interactions among spruce beetle disturbance, climate change and forest dynamics captured by a forest landscape model. *Ecosphere* 6:1–20. https://doi.org/10.1890/ES15-00394.1

Thom D, Rammer W, Seidl R (2017) Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. *Glob Chang Biol* 23:269–282. https://doi.org/10.1111/gcb.13506

Thom D, Seidl R, Steyrer G, et al (2013) Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. *For Ecol Manage* 307:293–302. https://doi.org/10.1016/j.foreco.2013.07.017

Torres-Muros L, Hódar JA, Zamora R (2017) Effect of habitat type and soil moisture on pupal stage of a Mediterranean forest pest (*Thaumetopoea pityocampa*). *Agric For Entomol* 19:130–138. https://doi.org/10.1111/afe.12188

Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849. https://doi.org/10.1358/dot.2011.47.2.1576694

van Lierop P, Lindquist E, Sathyapala S, Franceschini G (2015) Global forest area disturbance from fire, insect pests, diseases and severe weather events. *For Ecol Manage* 352:78–88. https://doi.org/10.1016/j.foreco.2015.06.010

Veblen TT, Hadley KS, Nel EM, et al (2006) Disturbance Regime and Disturbance Interactions in a Rocky Mountain Subalpine Forest. *J Ecol* 82:125. https://doi.org/10.2307/2261392

Vepakomma U, Kneeshaw D, St-Onge B (2010) Interactions of multiple disturbances in shaping boreal forest dynamics: A spatially explicit analysis using multi-temporal lidar data and high-resolution imagery. *J Ecol* 98:526–539. https://doi.org/10.1111/j.1365-2745.2010.01643.x

Verble RM, Stephan FM (2009) Occurrence of carpenter ants in ozark forests in relation to prescribed fire and stand variables. *South J Appl For* 33:42–45. https://doi.org/10.1093/sjaf/33.1.42

Ward NL, Masters GJ (2007) Linking climate change and species invasion: An illustration using insect herbivores. *Glob Chang Biol* 13:1605–1615. https://doi.org/10.1111/j.1365-2486.2007.01399.x

Ward SF, Kees AM, Maddox MP, et al (2019) The role of simulated spring water stress in interactions between eastern larch and larch casebearer. *Arthropod Plant Interact* 13:621–633. https://doi.org/10.1007/s11829-018-09670-z

Watt GA, Fleming RA, Smith SM, Fortin MJ (2018) Spruce budworm (*Choristoneura fumiferana* Clem.) defoliation promotes vertical fuel continuity in Ontario's boreal mixedwood forest. *Forests* 9:. https://doi.org/10.3390/f9050256

Watt GA, Stocks BJ, Fleming RA, Smith SM (2020) Stand breakdown and surface fuel accumulation due to spruce budworm (*Choristoneura fumiferana*) defoliation in the boreal mixedwood forest of central Canada. *Can J For Res* 9:1–9. https://doi.org/https://doi.org/10.1139/cjfr-2019-0076

Weed AS, Ayres MP, Hicke JA, et al (2013) Consequences of climate change for biotic disturbances in North American forests. *Ecol Monogr* 83:441–470. https://doi.org/10.1890/13-0160.1

Wermelinger B, Rigling A, Schneider Mathis D, Dobbertin M (2008) Assessing the role of bark- and wood-boring insects in the decline of Scots pine (*Pinus sylvestris*) in the Swiss Rhone valley. *Ecol Entomol* 33:239–249. https://doi.org/10.1111/j.1365-2311.2007.00960.x

Westlind DJ, Kelsey RG (2019) Predicting post-fire attack of red turpentine or western pine beetle on ponderosa pine and its impact on mortality probability in Pacific Northwest forests. *For Ecol Manage* 434:181–192. https://doi.org/10.1016/j.foreco.2018.12.021

Williams RS, Lincoln DE, Thomas RB (1994) Loblolly pine grown under elevated CO_2 affects early instar pine sawfly performance. *Oecologia* 98:64–71. https://doi.org/10.1007/BF00326091

Wong CM, Daniels LD (2017) Novel forest decline triggered by multiple interactions among climate, an introduced pathogen and bark beetles. *Glob Chang Biol* 23:1926–1941. https://doi.org/10.1111/gcb.13554

Woolley T, Shaw DC, Hollingsworth LT, et al (2019) Beyond red crowns: complex changes in surface and crown fuels and their interactions 32 years following mountain pine beetle epidemics in south-central Oregon, USA. *Fire Ecol* 15:. https://doi.org/10.1186/s42408-018-0010-z

Xu J, Budde KB, Hansen OK, et al (2018) Do silver fir woolly adelgids (*Dreyfusia nordmannianae*) facilitate pathogen infestation with Neonectria neomacrospora on Christmas trees (*Abies nordmanniana*)? *For Ecol Manage* 424:396–405. https://doi.org/10.1016/j.foreco.2018.05.006

Yamazaki K (2011) Gone with the wind: Trembling leaves may deter herbivory. *Biol J Linn Soc* 104:738–747. https://doi.org/10.1111/j.1095-8312.2011.01776.x

Yoneya K, Kugimiya S, Takabayashi J (2014) Leaf beetle larvae, Plagiodera versicolora (Coleoptera: Chrysomelidae), show decreased performance on uninfested host plants exposed to airborne factors from plants infested by conspecific larvae. *Appl Entomol Zool* 49:249–253. https://doi.org/10.1007/s13355-013-0243-x

Zhang Q -H, Byers J a., Zhang X -D (1993) Influence of bark thickness, trunk diameter and height on reproduction of the longhorned beetle, Monochamus sutor (Col., Cerambycidae) in burned larch and pine. *J Appl Entomol* 115:145–154. https://doi.org/10.1111/j.1439-0418.1993.tb00374.x

→02

CHAPTER 02

Predicting the potential distribution and impact of the invasive species *Cydalima perspectalis* in Europe

Quim Canelles
Emili Bassols
Jordi Vayreda
Lluís Brotons

This chapter has been published in *Ecology and Evolution*
(DOI: 10.1002/ece3.7476)

Abstract

Invasive species have considerably increased in recent decades due to direct and indirect effects of ever-increasing international trade rates and new climate conditions derived from global change. We need to better understand how the dynamics of early species invasions develop and how these result in impacts on the invaded ecosystems. Here we studied the distribution and severe defoliation processes of the box tree moth (*Cydalima perspectalis* W.), a tree defoliator insect native to Asia and invasive in Europe since 2007, through the combination of species distribution models based on climate and landscape composition information. The results showed that the combination of data from the native and the invaded areas was the most effective methodology for the appropriate invasive species modeling. The species was not influenced by overall landscape factors, but only by the presence of its host plant, dispersal capacity and climate suitability. Such climate suitability was described by low precipitation seasonality and minimum annual temperatures around 0°C, defining a continentality effect throughout the territory. We emphasize the need of studying distribution and severe defoliation processes separately because we identified that climate suitability was slightly involved in limiting species spread processes but strongly constrained ecosystem impact in terms of defoliation before the species reaches equilibrium with the new environment. New studies on habitat recovery after disturbance, ecological consequences of such impact and community dynamics in a context of climate change are required for a better understanding of this invasive species.

KEYWORDS
Biological invasion, box tree moth, ecological niche model, forest disturbance, habitat suitability

C. perspectalis distribution was defined by the presence of its host plant, its ability to spread, and its climate suitability

Introduction

The incidence of alien species to invaded host ecosystems has increased in recent years due to climate change and the growth in international trade (Hulme, 2003). The movement of alien species (not native to a specific location, also referred to as introduced or non-native species) has been linked to human activity for millennia due to international trade that favors the accidental introduction of species into new ecosystems (Bradshaw et al., 2016; Hulme, 2009). The association is so strong that key moments in history involving international commerce match alien species redistribution peaks, highlighting the end of the Middle Ages, the industrial revolution and, most remarkably, the recent era of market globalization (Hulme, 2009). The last 50 years have been characterized by an increase in transport networks and demand for commodities, allowing displacement of species into new ecosystems. This trend is more notable in countries with high economic activity, large transport infrastructure and facilitators of international commerce (such as dismantling of customs checkpoints in the case of European Union countries; Hulme, 2009; Roques et al., 2016).

Global warming is known to push changes in species distributional areas and may increase the probability that alien species become established and markedly impact new locations, becoming invasive species (alien species with an ecological or healthy impact). Many invasive species share traits such as short generation times, rapid dispersal or environmental plasticity that could be advantageous in a transitioning climate (Dukes & Mooney, 1999). Moreover, climate change may intensify the impact severity and likelihood of pest outbreaks, both in native and alien species (Bebber, Ramotowski, & Gurr, 2013; FAO, 2008). However, some scientists question the relevance of climate change on alien species performance, because its importance is equivalent to other factors such as land cover or geography of each site (Pyšek et al., 2010). They also argue that new climate conditions do not always lead to increasing the climate niche of alien species, because each species could perform differently in distinct areas (Bebber et al., 2013; Peterson, Papeş, & Soberón, 2008).

Biological invasions progress through the following consecutive phases: (1) arrival, (2) establishment, (3) dispersion and (4) impact (Vermeij, 1996). Only a small percentage of alien species eventually progress to the last stage when the species is considered invasive and causes damage to the environment, human economy or human health (Roques et al., 2016). However, their effects on the economy, society and ecology may be massive. Invasive insects (the second largest invasive group behind vascular plants; Seebens et al., 2017) are mainly studied because they cause economic and social damage in agriculture. The damage caused by invasive insect species in the forest industry is also significant, reaching $70 billion annually for the world (Bradshaw et al., 2016).

The ecological effects of invasive insect species occur at different levels of biological organization, from genetics (genetic hybridization with native species), to populations (new prey–predator relations) to ecosystems (phylogenic and taxonomic diversity, trophic networks, ecosystem productivity, etc.; Blackburn et al., 2014). Landscape may be directly affected by massive cases of herbivory leading plant species or entire ecosystems to high risk (e.g., the case of *Elatobium abietinum* W., which is invasive in North America and threatening to *Picea engelmannii*; Lynch, 2004). However, invasive insect species can also have indirect effects on communities, either by frustrating plant reproduction mechanisms (the case of *Lymantria dispar* L. causing oak seedling mortality both in native and invaded area; Gottschalk, 1989) or by triggering a cascade effect leading to the facilitation of other disturbances such as fire, arrival of other diseases or sensitivity to drought (Canelles, Aquilué, James, Lawler, & Brotons, 2021).

Management actions and policies are required to deal with invasive species impacts on ecosystem functioning and associated goods and services. Identifying the potential distribution and the stage of invasion of the studied species is critical for an adequate management strategy and quick development of action plans is required because eradication after the species establishment stage represents colossal costs and is often unsuccessful (Perrings, Dehnen-schmutz, Touza, & Williamson, 2005; Pimentel, Zuniga, & Morrison, 2005). Species distribution models (SDMs) are commonly used to predict the potential distribution range of invasive species (Uden, Allen, Angeler, Corral, & Fricke, 2015). SDMs are built on the general concept of a fundamental niche and predicted species distributions that depend on the modeling algorithm that is applied. Such algorithms are trained with a given species occurrence and associated environmental data and then projected onto different areas to identify regions with environmental suitability for such species (Elith & Leathwick, 2009; Guisan, Thuiller, & Zimmermann, 2017). However, the application of species distribution models to invasive species (SDMi) is under discussion because it may contradict two SDM assumptions: (1) ecological niches are stable in space and time and (2) the studied species is in quasi-equilibrium with the environment (Barbet-Massin, Rome, Villemant, & Courchamp, 2018; Elith & Graham, 2009; Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012; Gallien, Münkemüller, Albert, Boulangeat, & Thuiller, 2010). Thus, for an adequate understanding of the species, it is necessary to combine information from the original area and the invaded area as well as develop a synoptic view of the mechanisms involved in the invasion process, identify source populations, clarify invasive pathways and describe the main ecological factors and processes that favor or restrict invasive species performance (Bras et al., 2019; Kriticos et al., 2003; Pyšek et al., 2010). Moreover, differential description of species distribution (where the species is present) and severe damage dynamics (where the impact is high) may help accurate management strategies (Roques et al., 2016). To perform proper management, approaches must combine global and regional information of the invasive species as well as incorporate its processes dynamically (Hulme, 2003). Thus, cooperation between scientific researchers and managers is mandatory.

The box tree moth, *Cydalima perspectalis* W. (FIG. 1), native to Asia, is a prime example of an invasive alien species in Europe with a potential for high ecosystem impact. This species arrived in central Europe in 2007 and has spread throughout the continent (Kim & Park, 2013; Krüger, 2008; Maruyama & Shinkaji 1987). *C. perspectalis* causes economic and huge ecological effects because during its caterpillar phase it feeds on species of the genus *Buxus*, often leading to complete defoliation and producing significant damage to natural habitats as well as parks and gardens with ornamental boxwood fences. The persistence of consecutive defoliation episodes and the habit of caterpillars to eat the bark when there are no leaves may lead to the death of the plant (Artola, 2019; Mitchell, Chitanava, Dbar, & Kramarets, 2018; Straten & Muus, 2010). The ecological effects of *C. per-*

▶ **FIGURE 1**
Adult individual of *C. perspectalis*. Source: Jenny Llopis.

spectalis and consequent boxwood decay include the risk of species hosted in box trees (Mitchell et al., 2018) and the endangerment of some Mediterranean mountain ecosystems where the box tree is the main undercover species (Di Domenico, Lucchese, & Magri, 2012).

In this study, we aimed to identify the main determinants of *C. perspectalis* distribution and how these factors constrain distribution dynamics and ecosystem impact after the species establishment in a new environment. More specifically, we addressed the following questions: (1) Does the climate niche in the native area define the expansion process of the species in recently invaded areas? (2) Is the species distribution influenced by habitat composition (e.g., forest cover, habitat fragmentation, etc.) interacting with the climate niche? (3) Are the processes of spread and impact different in terms of the underlying factors that determine these dynamics?

Methods

STUDY SPECIES

The tree box moth *C. perspectalis* W (Lepidoptera: Crambidae), formerly placed in the genera *Glyphodes*, *Diaphania* and *Neoglyphodes* (Mally & Nuss, 2010), is a native insect from Asia, mainly China, Japan, Korea and India (Kim & Park, 2013; Maruyama & Shinkaji, 1987; Park, 2008). This species was first introduced in Europe in 2007, entering in Germany via the trade of ornamental box trees between China and Europe (Casteels et al., 2011; Leuthardt, 2013; Nacambo et al., 2014). In recent years, new observations have been recorded in Switzerland and the Netherlands (Leuthardt, 2013; Straten & Muus, 2010), and in a period of 10 years, the insect has spread all across Europe and into Asia Minor (Bras et al., 2019). Such spread is thought to be due to the flight capability of the species but mainly due to the accidental transport of individuals to different localities in Europe (Kenis, Roques, Timms, & Lopez-vaamonde, 2009; Matošević, 2013; Roques et al., 2016). According to its biological development, *C. perspectalis* has a classical egg–caterpillar–pupa–adult cycle. Adult mating phases start in the spring and end in the late summer with a cycle of 2–3 generations per year (Bakay & Kollár, 2018; Leuthardt, 2013; Nacambo et al., 2014; Nagy et al., 2017; Santi, Radeghieri, Inga Sigurta, & Maini, 2015), but up to 5 generations per year have been reported in China

(Chen et al., 2005). Temperature (minimum temperature and degree days) and relative humidity have usually been considered critical for species development (Suppo, Bras, & Robinet, 2020). Egg hatching success has been reported successful between 15 and 30°C in Asia (Maruyama & Shinkaji, 1987), while development threshold temperatures and degree days (dd) were 10.9°C and 45 dd for the egg stage; 8.4°C and 322 dd for the larval stage; and 11.5 °C and 133 dd for the pupal stage (Nacambo et al., 2014). In its native range, up to 10 different *Buxus* species have been documented as host plants, with a preference for *Buxus microphylla* Siebold & Zucc. (Maruyama, T. ; Shinkaji, 1991). In Europe, *C. perspectalis* is hosted on *Buxus sempervirens* L., a common species in southern and western European forests as well as a decorative plant in gardens throughout the continent (Artola, 2019; Bras et al., 2019; Wan et al., 2014).

STUDY AREA

The area of study was Catalonia, a 32,114 km2 region located in northeastern Spain with a predominantly Mediterranean climate. Its complex orography, with an altitude range from 0 to more than 3,000 m above sea level (a.s.l.) and a coast extending over 750 km, has resulted in a highly diverse climate. The region is extensively covered by forest (40%) and scrublands (16%), while agricultural lands (29%) and urban areas (6%) contribute to the fragmentation of natural areas (Ibàñez, Burriel, & Pons, 2002). Forests are dominated by Aleppo pine (*Pinus halepensis* M.), Holm oak (*Quercus ilex* L.), Scots pine (*Pinus sylvestris* L.) and European black pine (*Pinus nigra* subsp. *salzmannii* A.), which together represent two thirds of the total forest surface in Catalonia. *B. sempervirens* is widely distributed in the study area, being essential for some of the ecosystem understory (because it is shade tolerant) but also frequent in open shrub areas. It is normally found in limestone of sub-Mediterranean environments, although it can be also found in subalpine and Mediterranean forests covering a range of 100–1,900 m a.s.l. (Folch, 1985).

Catalonia has a high concentration of exotic species due to the high population density—and consequent trade movements and anthropization of the landscape—and the moderate climate conditions (Gassó et al., 2009). The box tree moth was first observed in Catalonia in 2014 (Bassols Isamat & Oliveras Giralt, 2014), but 2017 was the first year of high severity defoliation recorded specifically in northeastern Catalonia. Since then, the species has spread through the center of the territory.

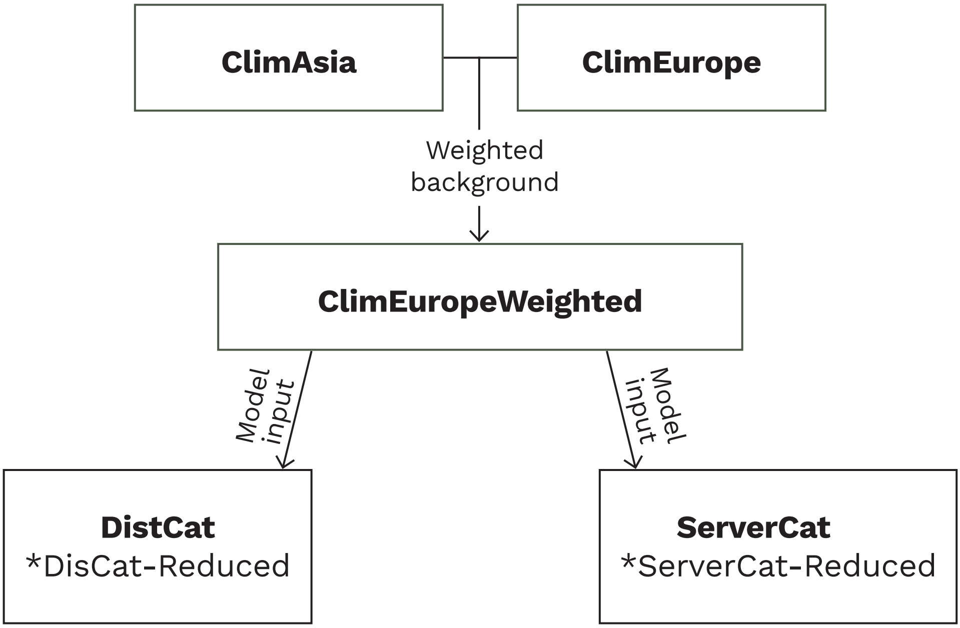
GENERAL OVERVIEW OF MODELING

The research presented in this paper comprises different interconnected models (FIG . 2):

1. — Climate suitability model for the distribution of *C. perspectalis* calibrated in the native area, Asia (ClimAsia). This model is projected to Asia and Europe.

2. — Climate suitability model for the distribution of *C. perspectalis* calibrated in the invaded area, Europe (ClimEurope). This model is projected to Europe and Asia.

3. — Climate suitability model for the distribution of *C. perspectalis* calibrated in the invaded area, Europe, but background information weighted with the ClimAsia projection in Europe (ClimEuropeWeighted). This model is projected to Europe and Asia.



▶ **FIGURE 2**
Conceptual diagram of the different models included in the study and the established relationship between them.

4. — Distribution model in Catalonia (DistCat). This is an ecological niche model that uses previous ClimEuropeWeighted output and other information as input variables. A variation of this model using fewer input variables was built (DistCat-Reduced).

5. — Severe defoliation model in Catalonia (SeverCat). This is an ecological niche model that uses previous ClimEuropeWeighted output and other information as input variables. A variation of this model using fewer input variables was built (SeverCat-Reduced).

The above-mentioned models are based on the SDM methodology (Guisan, Thuiller, & Zimmermann, 2017). Modeling code is available at https://github.com/quimcanellestrabal/Cydalima_QuimCanelles.

CLIMATE SUITABILITY MODEL APPROACH (CLIMASIA AND CLIMEUROPE)

Climate suitability models for *C. perspectalis* in Asia and Europe were built combining *C. perspectalis* occurrences and associated environmental data. Occurrence data of *C. perspectalis* at the global level were obtained from the Global Biodiversity Information Facility (GBIF, 2020) and complemented with literature citations (Kim & Park, 2013; Wan et al., 2014). Information was accurately selected by discarding observations with incomplete information, without associated quality coordinates, spatially clustered records, and duplicated locations. A final set of 83 and 3,074 occurrence data were obtained from Asia and Europe, respectively. To calibrate the climate suitability model, 10,000 randomly generated background points were created in each model extent (ClimAsia extent: longitude = 95 to 150, latitude 20 to 45; ClimEurope extent: longitude = -15 to 50, latitude = 35 to 75; Elith et al. 2011; Phillips et al. 2009).

We regressed the presence/absence of *C. perspectalis* models for Asia and Europe with eight explanatory climate variables obtained from CHELSA (Karger, 2017) at 30 arc seconds (ca. 1,000 m) spatial resolution and mean values for 1979–2013 (TABLE 1). These eight variables were the final selection from an initial set of 19 climate variables that were subjected to a multicollinearity test using Pearson's correlation coefficient and variance inflation factor (VIF) analysis both in Asian and European regions (Marquaridt, 1970). We finally selected only one variable from each set of highly correlated variables ($|r| > 0.7$; VIF > 10) depending on its

▶ **TABLE 1**
Summary of variables used in each model.

VARIABLE	**TYPE**	**MODEL**
Mean diurnal range (bio2) [°C]	Bioclimatic	ClimaAsia, ClimEurope and ClimEuropeWeighted
Max temperature of warmest month (bio5) [°C]		
Min temperature of coldest month (bio6) [ºC]		
Annual precipitation (bio12) [mm/year]		
Precipitation seasonality (bio15) [coefficient of variation]		
Precipitation of driest quarter (bio17) [mm/quarter]		
Precipitation of warmest quarter (bio18) [mm/quarter]		
Precipitation of coldest quarter (bio19) [mm/quarter]		
Climatic suitability [%]		DistCat and SeverCat
Elevation [m]	Topographic	
Aspect [N-W-S-E categories]		
Forest cover 1km radius [%]	Habitat composition	
Mean basal area at 1km radius [m2*ha-1]		
Habitat fragmentation (nº landscape patches / nº habitat classes)		
Habitat heterogeneity (nº landscape patches * nº habitat classes)		
Buxus sempervirens cover 10km radius [%]		
Min distance to *C. perspectalis* observations [m]	Dispersion	DistCat
Min distance to high severity *C. perspectalis* observations [m]		SeverCat

relative contribution to the overall model and corroborated by the described biological relevance to the studied species in the literature (Artola, 2019; Nacambo et al., 2014).

Climate suitability models for *C. perspectalis* in Asia and Europe were assembled by the species distribution modeling algorithm MaxEnt in R 3.6.1 (R Core Team, 2019), with the *dismo* (Hijmans, 2017) and the *maxnet* (Phillips, 2017) packages. MaxEnt is a machine learning algorithm used for describing probability distributions following the principle of maximum entropy, subject to restraints imposed by the presence of species and their surrounding environment (Phillips et al., 2009). Modifying MaxEnt algorithm parameters so that they are adequate for each study is highly recommended (Elith et al., 2011; Merow, Smith, & Silander, 2013; Morales, Fernández, & Baca-González, 2017). Thus, according to the sample size, the broad extension, and the limited knowledge of the studied species, we parametrized the MaxEnt algorithm with β-multiplier = 3, discarding the use of threshold prediction and featuring predictors with quadratic response curves. We realized a sample data-splitting procedure for evaluating the model. First, models were calibrated with 70% of the initial data. Second, models were run 10 times taking the average as the final model. Finally, models were evaluated on the remaining 30% of initial data with two model evaluations: the area under the receiver operating characteristic curve (AUC; Hanley & Barbara J. McNeil, 1982) and the continuous Boyce index (CBI; Boyce, Vernier, Nielsen, & Schmiegelow, 2002). AUC values are between 0 and 1, where values close to 0.5 are equivalent to a random prediction, values greater than 0.8 are considered a reliable prediction and values up to 1 represent perfect agreement of the model with the observed data (Fielding & Bell, 1997). CBI values are continuous between -1 and +1, where positive values indicate a model that presents predictions consistent with the distribution of occurrences in the evaluation, values close to zero indicate a model equivalent to a random model and negative values indicate counter predictions (e.g., predicting no occurrence in areas where actual presence is recorded; Hirzel et al. 2006; Manzoor, Griffiths, and Lukac 2018).

Because invasive species are not in equilibrium with the invaded area, there are climatically suitable locations in which the species may not have arrived yet due to dispersal constraints and the invasion story. Hence, background sample considered in the model may include both “true” and “false” absences (Gallien et al., 2012). To analyze the adequacy of the models, we checked the ClimEurope model adequacy when projected in Asia and ClimAsia when projected in Europe (Srivastava, Griess, & Keena, 2020). Finally, another SDM model called ClimEurope-Weighted was calibrated with occurrence data from Europe (the same that were used in ClimEurope) but background data were weighted with the ClimAsia projection in Europe. Weights for each background point (x) were obtained from the formula presented by Gallien et al. (2012):

$$\text{Weight (x)}= \frac{1}{1+\left(\frac{\text{ClimAsia projection in Europe (x)}}{\text{ClimAsia projection in Europe (x) - 1}}\right)^{2}}$$

The highest weight values (i.e., a low habitat suitability) were attributed to a background sample that showed a high level of agreement with the ClimAsia model projection (i.e., it probably represents a “true” absence). Comparison of these three approaches through respective output value correlations, AUC and CBI evaluations and climate variable response curves allowed us to analyze the data to define the distribution of the species in the native and invaded area.

ECOLOGICAL NICHE MODEL FOR DISTRIBUTION AND SEVERE DEFOLIATION

We built two models of potential distribution and severe defoliation (as an indicator of ecosystem impact) in Catalonia, where controlled quality data and distribution dynamics were more manageable than on a global scale. Occurrence data used in Catalonia were obtained from the community science project Alerta Forestal (AF), a collaborative tool where users upload field observation of forest disturbances (fire, drought, or some forest pests) providing a picture, its coordinates, and the level of disturbance severity (low, moderate, high, and very high according to the percentage of defoliation). We combined AF data with observations obtained from forest rangers (Agents Rurals de la Generalitat de Catalunya) in 2018 and 2019 that sampled boxwood locations all along the study area (avoiding sampling bias) and also reported the level of disturbance severity (four levels according to the percentage of defoliation, equivalent to AF data). Data quality was checked by discarding observations with no associated quality coordinates, wrong locations or species identification and spatially clustered records. Disturbance severity levels were subsequently evaluated by experts reviewing the percentage of defoliation using the picture facilitated. Two final sets of 566 and 1,022 occurrence data points were collected in Catalonia during 2018 and 2019, respectively. We generated a random located set of 10,000 background points in Catalonia to calibrate the models.

Potential distribution and severity were defined with the use of biotic and abiotic variables (TABLE 1), which were selected according to ecological descriptions of the species (Artola, 2019; Nacambo et al., 2014; Roura-Pascual, Brotons, García, Zamora, & De Càceres, 2012). Abiotic variables were defined by elevation and aspect variables obtained from the Digital Elevation Model of the Spanish National Geographic Institute (Ministerio de Fomento, 2011) as a topographic approximation and the ClimEuropeWeighted model projection as a summary of relevant climate information.

Biotic determinants were defined by the amount of suitable habitat composition for the species, as they are demonstrated to improve species distribution modeling (Meier et al., 2010; Stanton, Pearson, Horning, Ersts, & Reşit Akçakaya, 2012). First, we calculated the percentage of forest and the mean basal area at a 1 km radius around every observation plot, obtained from *Variables Biofísiques de l'Arbrat de Catalunya* (Bozal & Orriols 2016). Second, we calculated the habitat fragmentation and habitat heterogeneity from the number of patches and habitat classes per square kilometer considered in the Land Cover Map of Catalonia (Ibàñez et al., 2002). We finally included the percentage of the host species *B. sempervirens* at a 10 km radius around each plot (that is the reported maximum flight distance per year for *C. perspectalis* adults; Bras et al. 2019; Straten & Muus 2010). Boxwood presence was defined by the combination of occurrences reported in the Fourth Spanish National Forest Inventory (IV IFN, 2008–2017) and the Map of Habitats of Catalonia (Carreras, 2004; Carreras, Ferré, Oliva, & Pérez-Prieto, 2014).

To define the dispersal capability of the species, we calculated the distance between each 2019 species observation and the closest 2018 observation. For defoliation severity dynamics of *C. perspectalis* (SeverCat model), we repeated the same methodology but selected only high severity observations of 2018 and 2019 and calculated the minimum distance to such points. All variable information for SeverCat and DistCat models were prepared at a 1 km pixel resolution.

The potential distribution model was calibrated with the occurrence data from 2019 and climatic, topographic, habitat composition and map of distances for 2018 as explanatory variables, using the MaxEnt algorithm in R 3.6.1 (R Core Team, 2019), with the *dismo* (Hijmans, 2017) and the *maxnet* (Phillips, 2017) packages. The severity defoliation model was also calibrated with occurrence data from 2019 and the same explanatory variables but using map of distances to high severity points for 2018. Once again, models were calibrated with 70% of initial data and evaluated with the remaining 30% and AUC and CBI validation.

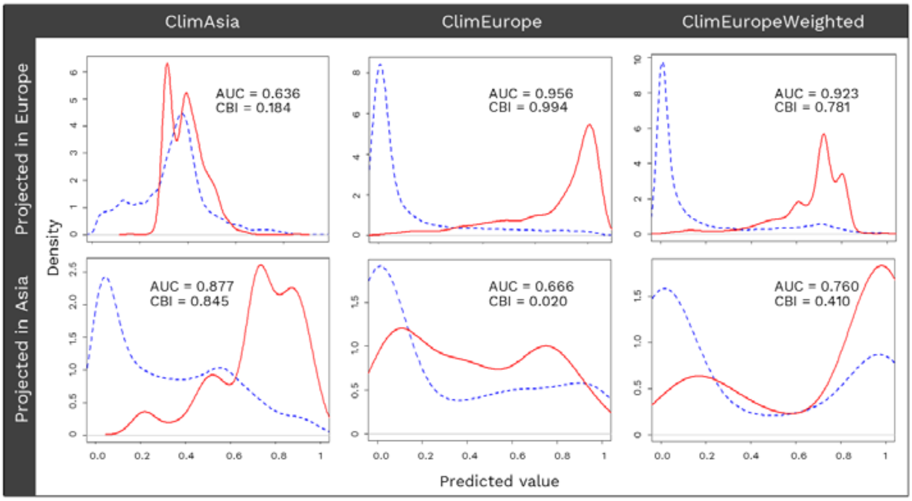
The distribution of *C. perspectalis* may be limited to the distribution of its host plant and dispersal story (i.e., distance between observations). To analyze the relevance of the other variables, we generated the models DistCat-Reduced and SeverCat-Reduced that were repetitions of previous models but using a new background set randomly distributed in a 10 km buffer around each presence (thus eliminating the distance factor; Gallien et al., 2012; Phillips et al., 2009) and masking only the locations with the presence of boxwood (thus eliminating this factor).

Results

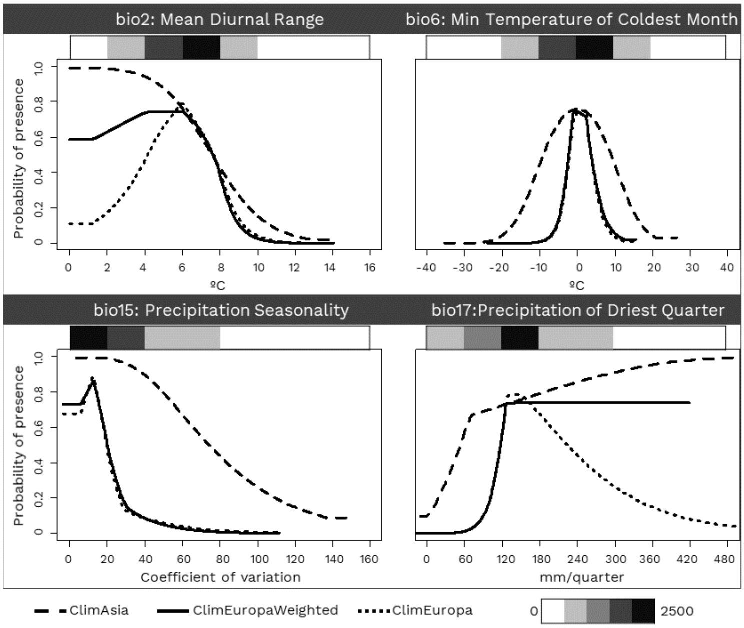
DEALING WITH NON-EQUILIBRIUM IN THE INVADED AREA

Three approaches were used to evaluate the adequacy of the data defining *C. perspectalis* distribution in the invaded area. The ClimaAsia model had an AUC of 0.88 and a CBI of 0.85 in the native area, but 0.64 and 0.18, respectively, when projected to Europe (FIG . 3). The ClimEurope model achieved good performance when projected in Europe (AUC = 0.96 and CBI = 0.99), but its evaluation fell to 0.67 and 0.02, respectively, when applied to Asia. Finally, the ClimEuropeWeighted model scored an AUC of 0.92 and a CBI of 0.78 in Europe and 0.76 and 0.41, respectively, when projected to Asia.

When analyzing the response curves for the main variables, similar variable contributions were found in the different models. However, in general, ClimAsia accounted for a wider range of values for each variable than ClimEurope, while ClimEuropeWeighted was in between the other two (FIG. 4).



▶ FIGURE 3
The density of predicted values for background sample (slash) and occurrences (line) according to each climate model projected in Asia and Europe. The area under the receiver operating characteristic curve (AUC) and continuous Boyce index (CBI) scores are added to each model and projection.



▶ FIGURE 4
Response curves showing how the four main environmental variables affects each climate model prediction for *C. perspectalis*. These response curves are the mean of 10 runs performed for each model. Grey heatmaps indicate the number of real observations found in every value range.

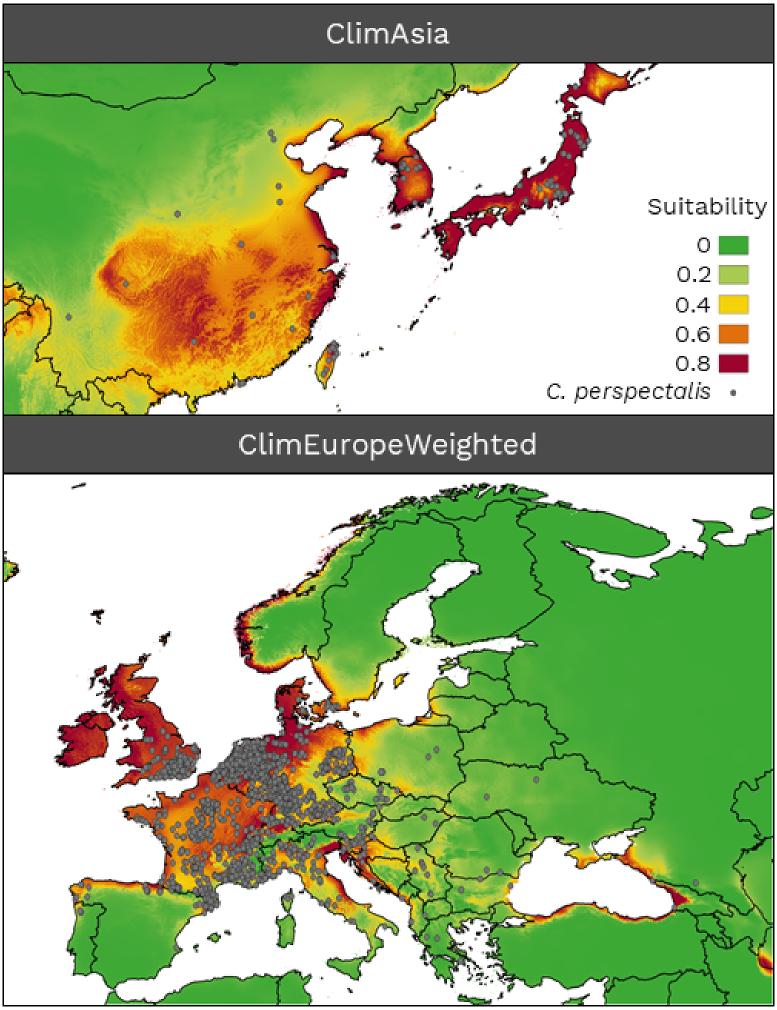
CLIMATE SUITABILITY IN THE NATIVE AND INVADED AREAS

Heuristic estimation of the relative contribution of each climate variable defined Precipitation of driest quarter (bio17), Min temperature of coldest month (bio6), Precipitation seasonality (bio15; that is, the temporal distribution of precipitation on a monthly basis) and Mean diurnal range (bio2; that is, the annual mean of the difference between the maximum and minimum daily temperature) as the main explanatory variables both in ClimAsia and ClimEurope (FIG . 4). These four variables combined accounted for 87.6% and 94.3%, respectively, of the variability in the climatic models. According to the model, the most suitable areas for *C. perspectalis* are those with precipitations over 90 mm in the driest quarter and low coefficient of variation of precipitation during the year. Mild temperatures (annual minimal between -2 and 2ºC) and low diurnal variation (lower than 12ºC) may favor the presence of *C. perspectalis*.

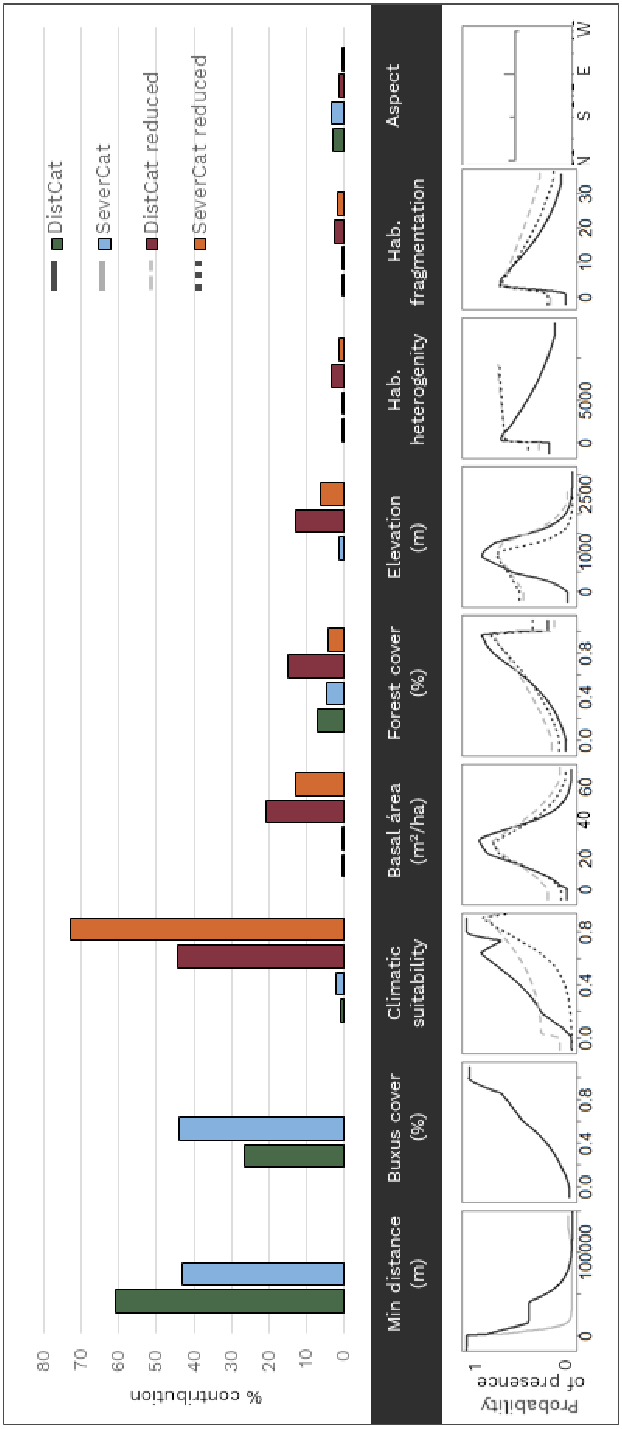
These variables defined the area of high suitability for *C. perspectalis*, including southeastern China, Taiwan, Japan and North and South Korea in the native area (FIG . 5). There is an apparent trend toward continentality for both the Asian and European species distributions. In the invaded area, central European countries including the United Kingdom were the main suitable areas for the species (FIG. 5). Here again, in the Mediterranean Sea, the Cantabrian Sea, the Black Sea, the Baltic Sea and the North Sea, continentality seemed to be relevant. The main mountain ranges such the Alps, the Pyrenees, the Balkans, and the Carpathian were excluded as suitable areas for the species.

ECOLOGICAL NICHE

Ecological niche models for *C. perspectalis* in Catalonia showed good adjustment with the observed data (DistCat, AUC = 0.90 and CBI = 0.92; SeverCat, AUC = 0.89 and CBI = 0.90). Boxwood cover and Min distance to *C. perspectalis* observations in the previous year were the two main variables that explained the distribution of the species and severe defoliation (FIG . 6). These two variables combined accounted for 86% and 87.2% of the variability of the DistCat and SeverCat models, respectively, diminishing the effect of other variables. Response curves indicated that the probability of presence of the species and the severity of defoliation increased almost linearly with the increase in the boxwood cover, while this probability



▶ FIGURE 5
Maps of climate suitability for *C. perspectalis*. in the native area (according to the ClimAsia model) and the invaded area (according to the ClimEurope-Weighted). Grey points indicate known species occurrences while color legend indicates the suitability index.



▸ FIGURE 6
Estimates of the relative contribution and response curve of each ecological variable to each ecological niche model for *C. perspectalis* in Catalonia.

decreases as Min distance to *C. perspectalis* observations were longer than 15 km for DistCat and 40 km for SeverCat.

The execution of the DistCat-Reduced and SeverCat-Reduced models revealed the role of other variables beyond the presence of boxwoods and the distance between observations of *C. perspectalis*. Both models showed good adjustment with the observed data (DistCat-Reduced, AUC = 0.75 and CBI = 0.68; SeverCat-Reduced, AUC = 0.80 and CBI = 0.74). Climate suitability was the main variable in both models, followed by mean basal area and the forest cover. Elevation was marginally relevant while aspect, habitat heterogeneity and habitat fragmentation variables did not provide additional information to the model (FIG. 6).

REGIONAL DISTRIBUTION AND SEVERE DEFOLIATION

Although comparison of models for the distribution of *C. perspectalis* (DistCat) and the severity of defoliation (SeverCat) had similar patterns both in the contribution of the explanatory variables and in the resulting maps, some differences must be noted (FIG. 6). Boxwood cover relevance in the DistCat model was half that of the contribution of distance between observations (27% and 59%, respectively). Both variables were similarly relevant in the SeverCat model (44% and 43%, respectively). The additional contribution of other variables was minimal in both models. Ignoring boxwood cover and distance between observations, the SeverCat-Reduced model was more closely related to the climate suitability variable (73%) than any habitat composition factors (none higher than 13%). In addition, the SeverCat-Reduced model revealed an exponential relationship with climate suitability variable, increasing the severe defoliation probability when the climate suitability value was higher than 0.5 (FIG. 6). By contrast, variable contributions in the DistCat-Reduced model were more balanced (44% for the climate suitability variable, 21% for basal area and 15% for forest cover), and the relationship between model performance and the climate suitability variable was almost linear from 0 to 1. Additional contribution of aspect and habitat fragmentation and heterogeneity variables were poor in all four models.

Observations of *C. perspectalis* in 2018 in Catalonia occurred in the eastern interior of the region, while observations in 2019 expanded further west and south. Thus, the DistCat and SeverCat models for 2019 and their projections for 2020 produced maps with this same trend toward the western portion of the territory. Our models defined 541,000 ha of the distribution area and 317,000 ha of severe defoliation for *C. perspectalis* in 2019, while projections to 2020 predicted 643,000 ha and 380,00 ha, respectively (FIG. 7). These areas remain strongly related to the spatial coincidence of the boxwood distribution area with locations of high climate suitability for *C. perspectalis* (FIG. 8).

Discussion

REALIZED REGIONAL NICHE VERSUS GLOBAL NICHE

The application of SDMs to invasive species is controversial because invasive species are still expanding and not in equilibrium with the novel environment (Gallien et al., 2012). To address this issue, we compared three climate models considering realized regional niches (range of conditions actually occupied by a given species) in the native area (ClimAsia) and the invaded area (ClimEurope) and the combination of both, estimating the global niche (ClimEuropeWeighted; Gallien et al. 2012; Roura-Pascual et al. 2009; Uden et al. 2015).

Climate models developed from occurrence data in Asia (ClimAsia) and Europe (ClimEurope) resulted in good quality adjustment in respective calibration areas but were not reliable on a worldwide scale. Differences between these two models were explained because the presence in Asia covered a wider range of values in the considered climate variables and, therefore, presented a wider climate niche than ClimEurope. This is a case of niche shift in biological invasion and it is widely discussed in distribution and invasion studies (Zhang, Mammola, McLay, Capinha, & Yokota, 2020). Niche variation may correspond to the fact that the species in its native area had more time to expand and to be in pseudo-equilibrium with the environment (Gallien et al., 2012), although the small number of occurrences collected in Asia for this species may increase such an effect (Hernandez, Graham, Master, & Albert, 2006; Wisz et al., 2008). Consequently, the ClimAsia model applied to Europe did not provide a good match because it considered many false positives (causing specificity problems). Moreover, although the ClimEurope model provided good adjustment in Europe, it overestimated false negatives when analyzed globally (causing sensitivity problems). Thus, using only one estimate of realized regional niches (the native or the invaded area) may misrepresent the environmental preferences of the species and may lead to incomplete predictions (Broennimann et al., 2012; Fitzpatrick, Weltzin, Sanders, & Dunn, 2006).

The combination of information through the realized regional niche background sample weighted with the global niche information increased prediction accuracy and thus limited the influence of false negatives, maintaining the true positives of the regional model and letting climate variables at the regional level refine the model. Thus, the ClimEuropeWeighted model perfectly matched occurrences in Europe and estimated that the niche of *C. perspectalis* may be slightly wider than the realized niche. Hence, the species still has space for expansion.

ECOLOGICAL NICHE

In this study, we have presented a modeling design that considered the dispersal limitations of the species, the biotic environment (including community constrains) and the abiotic environmental conditions (including climate suitability) because the combination of these influences determines species occurrence in a given space area (Lortie et al., 2004; Sóberon, 2007). Dispersal processes were approximated with distance between observations; this variable accounted for the species distribution and impact as identified by the DistCat and SeverCat models. *C. perspectalis* observations were usually grouped, normally not exceeding a 15 km distance. This aggregation pattern is common in invasive species, which increase their radius of dispersal more rapidly in the early years of invasion (Roques et al., 2016). However, human-induced dispersion is a critical factor in the distribution of *C. perspectalis* and may facilitate a faster dispersal rate than estimated by the models.

As expected, boxwood cover was also a key factor for understanding the species distribution and severe defoliation. *C. perspectalis* is totally dependent on boxwood as a host species and does not develop on other host plants (Straten & Muus, 2010). Thus, this biotic factor may limit the distribution of *C. perspectalis* but at the same time accentuate the risk for the boxwood in the territory. In addition, boxwoods are usually used in gardening (parks, cemeteries, private gardens, etc.) and may play a key role of connectors between boxwood forests. Other biotic factors (habitat descriptors in terms of fragmentation and heterogeneity) were considered but were not relevant for the distribution or severity of *C. perspectalis*. These findings indicate that this species is a non-habitat specialist, similar to other species (Litvinchuk et al., 2014; Sardà-Palomera & Vieites, 2011; Vallecillo, Brotons, & Thuiller, 2009). Forest cover and mean basal area were also considered as habitat descriptors as well as for their influence on microclimatic conditions (direct radiation, forest temperature, etc.) that may affect insect development (Notter-Hausmann & Dorn, 2010). Species distribution was sensitive to these factors, performing a better response in areas of high forest cover and basal area between 20 and 30 m2/ha, and this may suggest that *C. perspectalis* performs better on understory boxwood than on open shrub areas. However, such a relation should be specifically questioned because observations and severe defoliation by the species were observed in both habitat types as confirmed by Danés et al. (n.d.) and Artola (2019).

Abiotic environmental conditions were considered through climate suitability and the two topographic variables. The use of climate suitability as a model input summarizing all climate information is increasingly relevant in ecological research (Jaime, Batllori, Margalef-Marrase, Pérez Navarro, & Lloret, 2019). Although climate suitability was not related to the species distribution and did not impact the DistCat and SeverCat models, it was the main factor when distance between observations and boxwood cover were excluded (i.e., climate is critical once the species arrives in a boxwood area). Climate models described *C. perspectalis* suitability through mild climate conditions, with low precipitation seasonality combined with a small temperature diurnal range. The relevance of those climatic variables has also been emphasized by other studies that identified climate conditions during the larval development as the key for the species success (Nacambo et al., 2014; Suppo, Bras, & Robinet, 2020). For example, the mean diurnal range may lead to a high degree day value (warmth above a development threshold temperature); this factor is highly related to insect development, as observed by Herms (2004) and Nacambo et al. (2014). Mild temperatures (minimum around 0) and low precipitation seasonality directly influence insect activity, growth and phenology (Jaworski & Hilszczański, 2014). In addition, low precipitation may indirectly affect the insect development by damaging the host plant and, thus, resource availability (Jaworski & Hilszczański, 2014; Zhu et al., 2014), but such interaction should be specifically studied for these species.

Exposed climate conditions defined the climate of western Europe and the British Isles (where precipitation during the dry period is over 200 mm/quarter) as well as the Atlantic Ocean, the Black Sea, the North Sea and the Mediterranean coasts (where there is little precipitation and temperature seasonality; Karger, 2017). Thus, climate suitability for *C. perspectalis* was characterized by a certain continentality effect, being more suitable in the coast than inland, both in its native and invasive area (FIG. 5); these findings had been identified by Nacambo et al. (2014). Although the elevation variable was not significant in our model, climate conditions defined lower climate suitability at higher elevations. The model indicates climatically suitable areas where the species is already found and areas where it has not been established (Ireland, Scotland, the coast of Norway and Sweden, etc.) but potentially could subject to the presence of boxwoods.

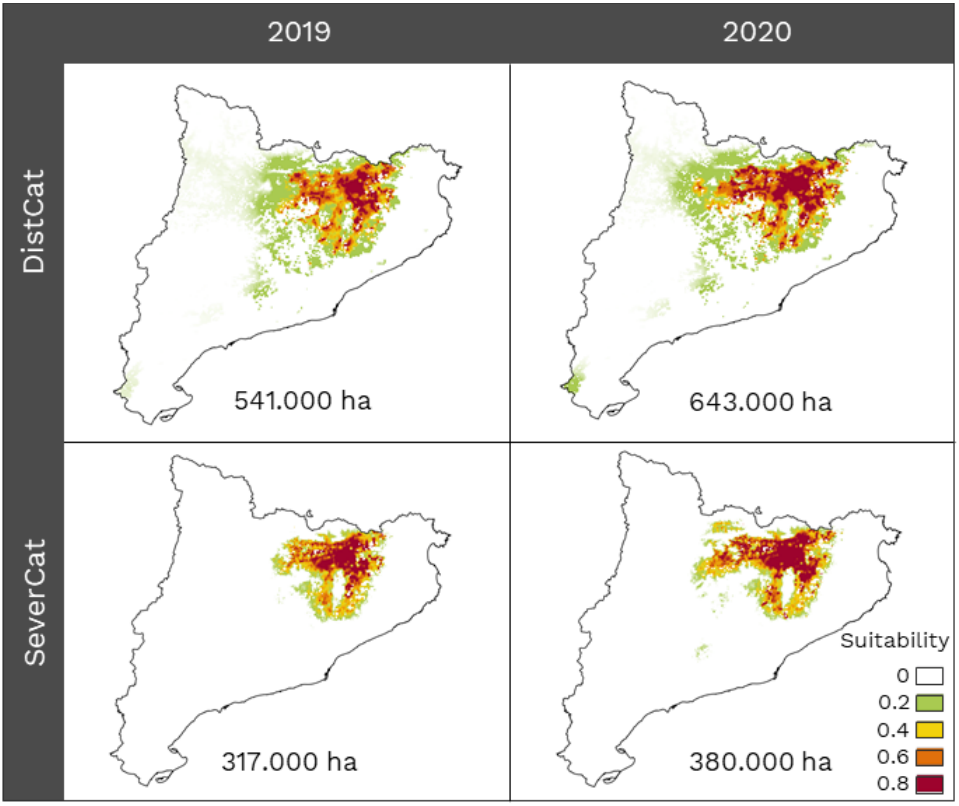
Finally, because precipitation seasonality and temperature are estimated to increase with climate change in the areas where the species is currently found (Karger, 2017), our results suggest that future conditions may affect the success of *C. perspectalis* (proposed in terms of phenology; Suppo, Bras, & Robinet, 2020) or even compromise its expansion and severity. Thus, the positive contribution of climate change on alien species performance is unclear (Bebber et al., 2013; Peterson et al., 2008).

INVASION STAGES: DISPERSION AND IMPACT

A description of the process by which *C. perspectalis* has invaded Catalonia is crucial to understand the invasion stage of the species (following the progress of arrival, establishment, dispersion, and impact). *C. perspectalis* has been continuously present in Catalonia since 2014, indicating that the arrival and establishment phases have been reached. Modeling distribution dynamics (as a proxy of dispersion) and defoliation severity (as a proxy of impact) separately allowed us to differentiate the mechanisms behind the two processes. Although both models showed high sensitivity to the same variables, climate suitability contributed more to the impact model (SeverCat), so this may be a mitigating factor for severe defoliation impact (i.e., the species could spread to different localities, but damage to the boxwoods would be severe only where there is higher climate suitability).

The output model maps indicated that areas of distribution and severe defoliation were linked: the higher the probability of occurrence of the species, the higher the defoliation impact (FIG. 7). Moreover, projections for 2020 indicated that potential areas to invasion and severe defoliation may increase at a similar rate. However, climate constraints to severe defoliation combined with the continentality pattern of climate suitability may reduce the inland advance of severe defoliation impact. This may cause slight asynchrony between the distribution and severe defoliation areas, as some occurrences were found far from the area of severe impact (FIG. 7), but pooled data from 2 years is not enough to check such patterns.

Natural enemies such as birds, bats, other insectivores or parasitoids may play an important role controlling the distribution of *C. perspectalis*, as happens with other invasive species (Snyder & Evans, 2006; Wanger et al., 2011). Wan et al. (2014) described the natural enemies of *C. perspectalis* in Asia, but in Europe only a few studies have covered this topic. Authors have described predation of *C. perspectalis* by *Passer domesticus* L., *Parus major* L., *Turdus merula* L. and *Ficedula albicollis* Tem (Bakay & Kollár, 2018). Moreover, *C. perspectalis* may interact with biotic diseases like fungi *Cylindrocladium* sp. (Henricot, Pérez Sierra, & Prior, 2000) altering both impacts on *B. sempervirens*, although this topic has not been studied to the date.



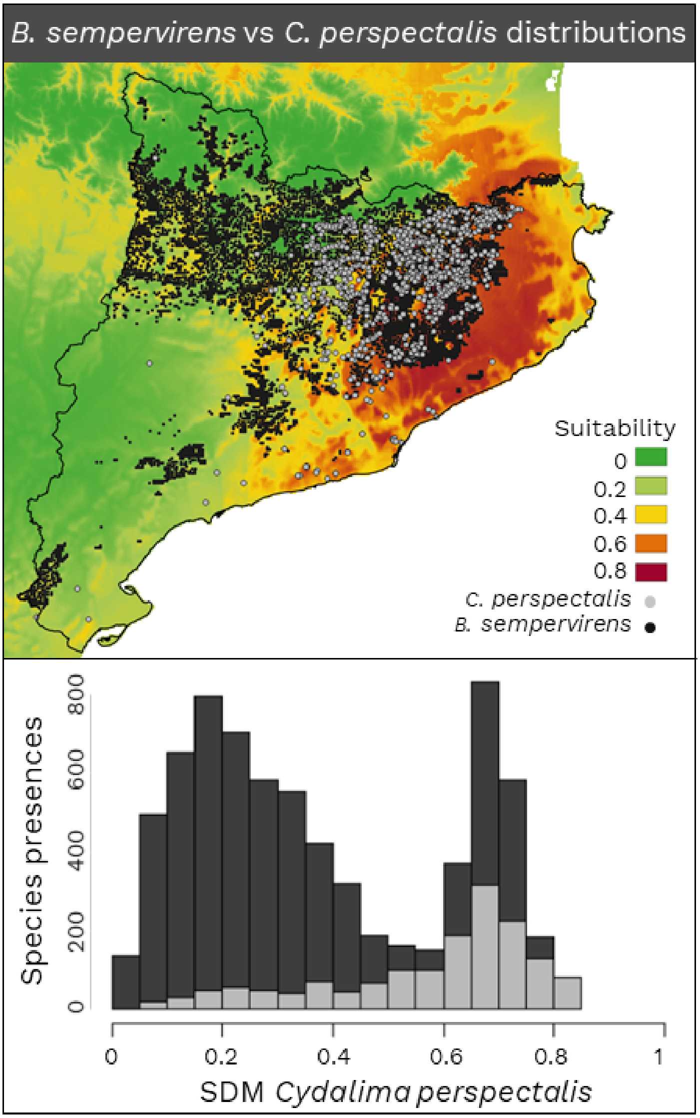
▶ FIGURE 7
The distribution model (DistCat) and the severe defoliation model (SeverCat) including areas afected for *C. perspectalis* in Catalonia for 2019 and projected to 2020. Maps are masked with the *B. sempervirens* distribution.

IMPACT AND MANAGEMENT

Consecutive defoliation periods of boxwoods by *C. perspectalis* may lead to host plant decay or death. Although boxwood can resprout after defoliation attacks, the synchrony between the generation of new leaves and the emergence of new insect generations (3–5 generations per year as mentioned above) compromises the viability of boxwoods (Artola, 2019; Straten & Muus, 2010). Boxwood loss has cultural, economic and ecological consequences (Mitchell et al., 2018). Ecologically, boxwoods host hundreds of species; indeed, 63 of them are found only in this host plant (Mitchell et al., 2018). At the landscape scale, boxwoods represent a key element of different Mediterranean habitats, both as an understory species and as dominant species in scrublands (Di Domenico et al., 2012). In Catalonia, boxwoods are abundant in 30% of the forest area (Carreras, 2004; Danés et al., n.d.) and are present in some singular forests (Comas, Gracia, & Vayreda, 2013). The loss of understory boxwoods may alter community dynamics by reducing inter-specific competition for soil water consumption or via fuel changes (in terms of both quantity and continuity) that could modify the fire regime in particular areas.

In the present study, climate suitability was described as an important variable in *C. perspectalis* distribution, but especially when defining high defoliation area, as mentioned in the previous section. Our results suggest that climate suitability is subject to a continentality effect (less suitability inland) and does not co-occur with boxwood distribution (FIG . 8). Thus, those boxwoods placed in areas with less favorable climatic conditions for the insect (i.e., inland and in high elevation) would be safe from high defoliation.

The impact of *C. perspectalis* on boxwoods concerns land managers. This study emphasizes that two key factors in the species distribution and impact are insect dispersal capability and climate suitability (considering boxwood presence). Because *C. perspectalis* cannot travel long distances by itself, the control of human activities (via commercial trades or via accidental anthropochorous transfer between forest areas) is crucial to limit the rapid expansion of the species. On the other hand, climate limitations have defined those areas most vulnerable to severe defoliation and, therefore, where protection efforts may be targeted. At the same time, the cultural value of particular forests should be valued to prioritize those singular areas of the territory.



▶ **FIGURE 8**

Spatial syncrony between *B. sempervirens* distribution (dark grey) and *C. perspectalis* distribution (light grey) according to climate suitability (color index on the upper panel).

Finally, it is necessary to question what the future of *C. perspectalis* in the invaded areas will be. When *C. perspectalis* impacts boxwoods in climatically suitable areas, its viability could be compromised due to food shortages. This could lead to a fatal decline in the population of the insect or to a cyclical relationship between boxwood defoliation–resprout and moth population dynamics. Hence, we emphasize the need for specific research that studies the viability of *C. perspectalis* and its host plant in the future.

Conclusions

In this study we found that the distribution of *C. perspectalis* mainly depends on the presence of its host plant and its ability to spread, so in the near future (with enough time for *C. perspectalis* to fully spread), all boxwoods might be affected by the insect. However, climate suitability may be a handicap for *C. perspectalis* development in some areas. The climatic niche is characterized by limited seasonality of precipitation and temperatures and low diurnal ranges, defining higher suitability in western Europe and in coastal areas. The case of *C. perspectalis* may not be favored by variations due to climate change, but climate niche projections would be necessary. Habitat descriptors and topographic variables were not relevant in our models; hence, this species is not habitat selective. However, the species is not in pseudo-equilibrium with the invaded environment, so the processes of interaction with new competitors and predator species is still unknown.

Understanding the invasion phases in the area of invasion is essential to differentiate the processes of dispersion and impact. We found that a high climate effect markedly impacts the process, indicating that in some areas where the species could spread, its impact may be mitigated due to unsuitable climatic conditions. This information is valuable when designing management plans, but questions remain regarding the boxwood resprout capability after defoliation or how *C. perspectalis* may interact with other disturbances.

References

Artola, J. (2019). Seguiment de la biologia i la fenologia de la papallona del boix (*Cydalima perspectalis*) al Parc Natural de la Sona Volcànica de la Garrotxa. *Generalitat de Catalunya; Departament de Territori i Sostenibilitat*.

Bakay, L., & Kollár, J. (2018). The spread rate of *Cydalima perspectalis* (Walker 1859) in Slovakia (2013-2015). *Plants in Urban Areas and Landscape*, 51–54. https://doi.org/https://doi.org/10.15414/PUAL/2018.51-54

Barbet-Massin, M., Rome, Q., Villemant, C., & Courchamp, F. (2018). Can species distribution models really predict the expansion of invasive species? *PLoS ONE*, *13*(3), 1–14. https://doi.org/10.1371/journal.pone.0193085

Bassols Isamat, E., & Oliveras Giralt, J. (2014). *Cydalima perspectalis* (Walker , 1859), una nova espècie invasora a Catalunya (Lepidoptera) : *Butll. Soc. Cat. Lep.*, *105*, 71–78.

Bebber, D. P., Ramotowski, M. A. T., & Gurr, S. J. (2013). Crop pests and pathogens move polewards in a warming world. *Nature Climate Change*, (September), 1–4. https://doi.org/10.1038/NCLIMATE1990

Blackburn, T. M., Essl, F., Evans, T., Hulme, P. E., Jeschke, J. M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D.M., Sendek, A., Vilà, M., Wilson, J.R.U. Winter, M., Genovesi, P. & Bacher, S. (2014). A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biology*, *12*(5). https://doi.org/10.1371/journal.pbio.1001850

Bozal, M. C., & Orriols, A. J. (2016). Mapes de variables biofísiques de l'arbrat de Catalunya. *Generalitat de Catalunya; Institut Cartogràfic i Geològic de Catalunya*.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling*, *157*, 281–300.

Bradshaw, C. J. A., Leroy, B., Bellard, C., Roiz, D., Albert, C., Fournier, A., Barbet-Massin, M., Salles, J. M., Simard, F. & Courchamp, F. (2016). Massive yet grossly underestimated global costs of invasive insects. *Nature Communications*, 7. https://doi.org/10.1038/ncomms12986

Bras, A., Avtzis, D. N., Kenis, M., Li, H., Vétek, G., Bernard, A., Courtin, C., Rousselet, J., Roques, A. & Auger-Rozenberg, M. A. (2019). A complex invasion story underlies the fast spread of the invasive box tree moth (*Cydalima perspectalis*) across Europe. *Journal of Pest Science*, *92*(3), 1187–1202. https://doi.org/10.1007/s10340-019-01111-x

Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W., Fortin, M. J., Randin, C., Zimmermann, N. E., Graham, C. H. & Guisan, A. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, *21*(4), 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

Canelles, Q., Aquilué, N., James, P. M. A., Lawler, J., & Brotons, L. (2021). Global review on interactions between insect pests and other forest disturbances. *Landscape Ecology*, 7. https://doi.org/10.1007/s10980-021-01209-7

Carreras, J. (2004). La cartografia dels hàbitats de Catalunya: una eina per conèixer i gestionar el territori. *Omnis Cellula*, 7, 52–56.

Carreras, J., Ferré, A., Oliva, F., & Pérez-Prieto, D. (2014). Avaluació dels canvis dels canvis en els hàbitats en els hàbitats a a Catalunya Catalunya. *Generalitat de Catalunya*, *Ed*. Retrieved from http://hdl.handle.net/2445/95855

Chen H.L., Gao Z.G., Zhou J.M. & Chen H.M. (2005). Bionomics of the box tree pyralis, *Diaphania perspectalis* (Walker). *Ji- angxi Plant Prot*. 28, 1–4.

Comas, L., Gracia, M., & Vayreda, J. (2013). Inventari de boscos singulars de Catalunya. *L'Atzavara*, *0*(22), 29–36.

Danés, A., Roura-Pascual, N. & Bassols, E. (n.d.). Estudi de la capacitat de rebrotada del boix (*Buxus sempervirens*) afectat per la papallona del boix (*Cydalima perspectalis*) a la comarca de la Garrotxa .

Di Domenico, F., Lucchese, F., & Magri, D. (2012). Buxus in Europe: Late Quaternary dynamics and modern vulnerability. *Perspectives in Plant Ecology*, *Evolution and Systematics*, *14*(5), 354–362. https://doi.org/10.1016/j.ppees.2012.07.001

Dukes, J. S., & Mooney, H. A. (1999). Does global change increase the success of biological invaders? *TREE*, *14*(4), 135–139. https://doi.org/https://doi.org/10.1016/S0169-5347(98)01554-7

Elith, J., & Graham, C. H. (2009). Do they? How do they? WHY do they differ? on finding reasons for differing performances of species distribution models. *Ecography*, *32*(1), 66–77. https://doi.org/10.1111/j.1600-0587.2008.05505.x

Elith, J., & Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

FAO. (2008). Salud y vitalidad de los bosques. 69–88. *Departamento de Montes de Recursos ForestalesDirección de Recursos Forestales (FAO)*, Roma, Italia. Retrieved from http://www.fao.org/docrep/013/i1757s/i1757s04.pdf

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, *24*(1), 38–49.

Fitzpatrick, M. C., Weltzin, J. F., Sanders, N. J., & Dunn, R. R. (2006). The biogeography of prediction error : why does the introduced range of the fire ant over-predict its native range? *Global Ecology and Biogeography*, 1–10. https://doi.org/10.1111/j.1466-822x.2006.00258.x

Folch, R.., Franquesa, T. & Camarasa, J. M. (1984). Història natural dels Països Catalans. 7. Vegetació. *Enciclopèdia Catalana.* Barcelona. 442 pp.

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N. E., & Thuiller, W. (2012). Invasive species distribution models - how violating the equilibrium assumption can create new insights. *Global Ecology and Biogeography*, *21*(11), 1126–1136. https://doi.org/10.1111/j.1466-8238.2012.00768.x

Gallien, L., Münkemüller, T., Albert, C. H., Boulangeat, I., & Thuiller, W. (2010). Predicting potential distributions of invasive species: Where to go from here? *Diversity and Distributions*, *16*(3), 331–342. https://doi.org/10.1111/j.1472-4642.2010.00652.x

Gassó, N., Sol, D., Pino, J., Dana, E. D., Lloret, F., Sanz-elorza, M., & Sobrino, E. (2009). Exploring species attributes and site characteristics to assess plant invasions in Spain. *Diversity and Distributions*, *15*, 50–58. https://doi.org/10.1111/j.1472-4642.2008.00501.x

GBIF Backbone Taxonomy (2019). *Cydalima perspectalis* (Walker, 1859). Checklist dataset *https://doi.org/10.15468/39omei* accessed via GBIF.org on 2020-06-01.

Gottschalk, K. W. (1989). Gypsy moth effects on mast production. *Proceedings of Southern Appalachian Mast Management Workshop*. University of Tennessee, Knoxville, Tennessee, USA., (June).

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). Habitat Suitability and Distribution Models With Applications in R. Cambridge University Press.

Hanley, J. A., & Barbara J. McNeil. (1982). The meaning and use of the area under a Receiver Operating Characteristic (ROC) curve. *Journal of Medical Internet Research*, *143*, 29–36. https://doi.org/10.1148/radiology.143.1.7063747

Henricot, B., Pérez Sierra, A., & Prior, C. (2000). A new blight disease on *Buxus* in the UK caused by the fungus *Cylindrocladium*. *Plant Pathology*, *49*(January), 805. https://doi.org/10.1046/j.1365-3059.2000.00508.x

Herms, D. (2004). Using degree-days and plant phenology. In *Minnesota Agricultural Experiment Station Publication* (pp. 49–59). https://doi.org/DOI: 10.1007/978-81-322-0974-4_25

Hernandez, P. A., Graham, C. H., Master, L. L., & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, *5*(June), 773–785. https://doi.org/https://doi.org/10.1111/j.0906-7590.2006.04700.x

Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J., & Hijmans, M. R. J. (2017). Package 'dismo'. *Circles*, *9*(1), 1-68.

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, *199*(2), 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017

Hulme, P. E. (2003). Biological invasions: Winning the science battles but losing the conservation war? *Oryx*, *37*(2), 178–193. https://doi.org/10.1017/S003060530300036X

Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, *46*(1), 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Ibàñez, J. J., Burriel, J. A., & Pons, X. (2002). El Mapa de Cobertes del Sòl de Catalunya: Una eina per al coneixement, la planificació i la gestió del territori. *Perspectives Territorials*, (3), 10–25.

Jaime, L., Batllori, E., Margalef-Marrase, J., Pérez Navarro, M. Á., & Lloret, F. (2019). Scots pine (*Pinus sylvestris* L.) mortality is explained by the climatic suitability of both host tree and bark beetle populations. *Forest Ecology and Management*, *448*(June), 119–129. https://doi.org/10.1016/j.foreco.2019.05.070

Jaworski, T., & Hilszczański, J. (2014). The effect of temperature and humidity changes on insects development their impact on forest ecosystems in the expected climate change. *Forest Research Papers*, *74*(4), 345–355. https://doi.org/10.2478/frp-2013-0033

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, P. & Kessler, M. (2017). Climatologies at high resolution for the Earth land surface areas. *Scientific Data*. 4 170122. *https://doi.org/10.1038/sdata.2017.122*

Kenis, M., Auger-Rozenberg, M. A., Roques, A., Timms, L., Péré, C., Cock, M. J., Settele, J., Augustin, S. & Lopez-Vaamonde, C. (2009). *Ecological effects of invasive alien insects*. 21–45. https://doi.org/10.1007/s10530-008-9318-y

Kim, J., & Park, I. K. (2013). Female sex pheromone components of the box tree pyralid, *Glyphodes perspectalis*, in Korea: Field test and development of film-type lure. *Journal of Asia-Pacific Entomology*, *16*(4), 473–477. https://doi.org/10.1016/j.aspen.2013.08.002

Kriticos, D. J., Brown, J. R., Maywald, G. F., Radford, I. D., Nicholas, D. M., Sutherst, R. W., & Adkins, S. W. (2003). SPAnDX: A process-based population dynamics model to explore management and climate change impacts on an invasive alien plant, Acacia nilotica. *Ecological Modelling*, *163*(3), 187–208. https://doi.org/10.1016/S0304-3800(03)00009-7

Leuthardt, F. L. G. (2013). Distribution , life history , food choice and chemical ecology of the invasive box-tree pyralid *Cydalima perspectalis*. University of Basel. Retrieved from http://edoc.unibas.ch/30962/1/Dissertation_LF.pdf#page=21

Litvinchuk, S. N., Schepina, N. A., Munkhbaatar, M., Munkhbayar, K., Borkin, L. J., Kazakov, V. I., & Skorinov, D. V. (2014). Distribution and conservation status of the Far Eastern tree frog, *Hyla japonica* Günther, 1859 in Mongolia and Transbaikalia (Russia). *Russian Journal of Herpetology*, *21*(4), 303–314. https://doi.org/https://doi.org/10.30906/1026-2296-2014-21-4-303-314

Lortie, C. J., Brooker, R. W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F. I., & Callaway, R. M. (2004). Rethinking plant community theory. *Oikos*, *107*(2), 433–438. https://doi.org/10.1111/j.0030-1299.2004.13250.x

Lynch, A. M. (2004). Western North American naturalist fate and characteristics of *Picea* damaged by Elatobium abietinum (Walker) (Homoptera: Aphididae) in the White Mountains of Arizona. *Western North American Naturalist*, *64*(1). Retrieved from https://www.jstor.org/stable/41717336

Mally, R., & Nuss, M. (2010). Phylogeny and nomenclature of the box tree moth , *Cydalima perspectalis* (Walker , 1859) comb . n ., which was recently introduced into Europe (Lepidoptera : Pyraloidea : Crambidae : Spilomelinae). *European Journal of Entomology*, *107*(3), 393–400. https://doi.org/10.14411/eje.2010.048

Manzoor, S. A., Griffiths, G., & Lukac, M. (2018). Species distribution model transferability and model grain size-finer may not always be better. *Scientific Reports*, *8*(1), 1–9. https://doi.org/10.1038/s41598-018-25437-1

Marquaridt, D. W. (1970). Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics*, *12*(3), 591–612. https://doi.org/10.1080/00401706.1970.10488699

Maruyama, T. ; Shinkaji, N. (1991). The life-cycle of the box-tree pyralid, *Glyphodes perspectalis* (Walker) (Lepidoptera: Pyralidae). II. Developmental characteristics of larvae. *Jpn. J. Appl. Entomol. Zool*, *43*(10), 8509–8515. https://doi.org/10.1303/jjaez.35.221

Maruyama, T., & Shinkaji, N. (1987). Studies on the life cycle of the box-tree pyralid, *Glyphodes perspectalis* (Walker) (Lepidoptera: Pyralidae). I. Seasonal adult emergence and developmental velocity. *Jpn. J. Appl. Entomol. Zool.*, *31*(3), 226–232.

Matošević, D. (2013). Box tree moth (*Cydalima perspectalis* , Lepidoptera ; Crambidae), new invasive insect pest in Croatia. *South-East Eur For*, *4*(2), 89–94. https://doi.org/https://doi.org/10.15177/seefor.13-09

Meier, E. S., Kienast, F., Pearman, P. B., Svenning, J. C., Thuiller, W., Araújo, M. B., Guisan, A. & Zimmermann, N. E. (2010). Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography*, *33*(6), 1038–1048. https://doi.org/10.1111/j.1600-0587.2010.06229.x

Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography*, *36*(10), 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Ministerio de Agricultura Pesca Alimentación y Medio Ambiente (2017). Cuarto Inventario Forestal Nacional: Cataluña. *Gobierno de España: Ministerio de Agricultura Pesca Alimentación y Medio Ambiente*.

Ministerio de Fomento. (2011). Modelo Digital de Elevaciones. Madrid: *Instituto Cartográfico Digital*.

Mitchell, R., Chitanava, S., Dbar, R., Kramarets, V., Lehtijärvi, A., Matchutadze, I., Mamadashvili, G., Matsiakh, I., Nacambo, S., Papazova-Anakieva, I., Sathyapala, S., Tuniyev, B., Vétek, G., Zukhbaia, M., & Kenis, M. (2018). Identifying the ecological and societal consequences of a decline in *Buxus* forests in Europe and the Caucasus. *Biological Invasions*, *20*(12), 3605-3620. https://doi.org/10.1007/s10530-018-1799-8

Morales, N. S., Fernández, I. C., & Baca-González, V. (2017). MaxEnt's parameter configuration and small samples: Are we paying attention to recommendations? A systematic review. *PeerJ*, *2017*(3), 1–16. https://doi.org/10.7717/peerj.3093

Nacambo, S., Leuthardt, F. L. G., Wan, H., Li, H., Haye, T., Baur, B., Weiss, R. M. & Kenis, M. (2014). Development characteristics of the box-tree moth *Cydalima perspectalis* and its potential distribution in Europe. *Journal of Applied Entomology*, *138*(1–2), 14–26. https://doi.org/10.1111/jen.12078

Nagy, A., Szarukan, I., Csabai, J., Molnar, A., Molnar, B. P., Z.Karpati, Szanyi, S. & Toth, M. (2017). Distribution of the box tree moth (*Cydalima perspectalis* Walker 1859) in the north-eastern part of the Carpathian Basin with a new Ukrainian record and Hungarian data. *Bulletin OEPP/EPPO*, *0*, 1–4. https://doi.org/10.1111/epp.12384

Notter-Hausmann, C., & Dorn, S. (2010). Relationship between behavior and physiology in an invasive pest species: oviposition site selection and temperature-dependent development of the Oriental fruit moth (Lepidoptera: Tortricidae). *Environmental Entomology*, *39*(2), 561–569. https://doi.org/10.1603/en09231

Park, I. K. (2008). Ecological characteristic of *Glyphodes perspectalis*. *Korean J Appl Entomol*, 299–301. https://doi.org/https://doi.org/10.5656/KSAE.2008.47.3.299

Perrings, C., Dehnen-schmutz, K., Touza, J., & Williamson, M. (2005). How to manage biological invasions under globalization. *TRENDS in Ecology and Evolution*, *20*(5). https://doi.org/10.1016/j.tree.2005.02.011

Peterson, A. T., Papeş, M., & Soberón, J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling*, *213*(1), 63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Phillips, S. (2017). Maxnet: Fitting 'maxent'species distribution models with 'glmnet'. *R package version 0.1*, *2*.

Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, *19*(1), 181–197. https://doi.org/10.1890/07-2153.1

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*, 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Pyšek, P., Jarošík, V., Hulme, P. E., Kühn, I., Wild, J., Arianoutsou, M., Bacher, S., Chiron, F., Didžiulis, V., Essl, F., Genovesi, P., Gherardi, F., Hejda, M., Kark, S., Lambdon, P.W., Desprez-Loustau, M.L., Nentwig, W., Pergl, J., Poboljšaj, K., Rabitsch, W., Roques, A., Roy, D. B., Shirley, S., Solarz, W., Vilà, M. & Winter, M. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(27), 12157–12162. https://doi.org/10.1073/pnas.1002314107

R Core Team (2019). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL *https://www.R-project.org/*.

Roques, A., Auger-Rozenberg, M. A., Blackburn, T. M., Garnas, J., Pyšek, P., Rabitsch, W., Richardson, D. M., Wingfield, M. J., Liebhold, A.M. & Duncan, R. P. (2016). Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. *Biological Invasions*, *18*(4), 907–920. https://doi.org/10.1007/s10530-016-1080-y

Roura-Pascual, N., Bas, J. M., Thuiller, W., Hui, C., Krug, R. M., & Brotons, L. (2009). From introduction to equilibrium: Reconstructing the invasive pathways of the Argentine ant in a Mediterranean region. *Global Change Biology*, *15*(9), 2101–2115. https://doi.org/10.1111/j.1365-2486.2009.01907.x

Roura-Pascual, N., Brotons, L., García, D., Zamora, R., & De Càceres, M. (2012). Local and landscape-scale biotic correlates of mistletoe distribution in Mediterraean pine forests. *Forest Systems*, *21*(2), 179. https://doi.org/10.5424/fs/2012212-02155

Santi, F., Radeghieri, P., Inga Sigurta, G., & Maini, S. (2015). Sex pheromone traps for detection of the invasive box tree moth in Italy. *Bulletin of Insectology*, *68*(1), 158–160.

Sardà-Palomera, F., & Vieites, D. R. (2011). Modelling species' climatic distributions under habitat constraints: A case study with *Coturnix coturnix*. *Annales Zoologici Fennici*, *48*(3), 147–160. https://doi.org/10.5735/086.048.0303

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., Kartesz, J., Kenis, M., Kreft, H., Kühn, I., Lenzner, B., Liebhold, A., Mosena, A., Moser, D., Nishino, M., Pearman, D., Pergl, J., Rabitsch, W., Rojas-Sandoval, J., Roques, A., Rorke, S., Rossinelli, S., Roy, H. E., Scalera, R., Schindler, S., Štajerová, K., Tokarska-Guzik, B., Van Kleunen, M., Walker, K., Weigelt, P., Yamanaka, T. & Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 1–9. https://doi.org/10.1038/ncomms14435

Snyder, W. E., & Evans, E. W. (2006). Ecological effects of invasive arthropod generalist predators. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 95–122. https://doi.org/10.1146/annurev.ecolsys.37.091305.110107

Sóberon, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, Vol. 10, pp. 1–9. https://doi.org/doi.org/10.1111/j.1461-0248.2007.01107.x

Srivastava, V., Griess, V. C., & Keena, M. A. (2020). Assessing the potential distribution of asian Gypsy moth in Canada: A comparison of two methodological approaches. *Scientific Reports*, *10*(1), 1–10. https://doi.org/10.1038/s41598-019-57020-7

Stanton, J. C., Pearson, R. G., Horning, N., Ersts, P., & Reşit Akçakaya, H. (2012). Combining static and dynamic variables in species distribution models under climate change. *Methods in Ecology and Evolution*, *3*(2), 349–357. https://doi.org/10.1111/j.2041-210X.2011.00157.x

Straten, M. J. Van Der, & Muus, T. S. T. (2010). The box tree pyralid, *Glyphodes perspectalis* (Lepidoptera: Crambidae), an invasive alien moth ruining box trees. In *Proceedings of the Netherlands Entomological Society Meeting*. (Vol. 21).

Suppo, C., Bras, A., & Robinet, C. (2020). A temperature- and photoperiod-driven model reveals complex temporal population dynamics of the invasive box tree moth in Europe. *Ecological Modelling*, *432*. https://doi.org/10.1016/j.ecolmodel.2020.109229

Uden, D. R., Allen, C. R., Angeler, D. G., Corral, L., & Fricke, K. A. (2015). Adaptive invasive species distribution models: a framework for modeling incipient invasions. *Biological Invasions*, *17*(10), 2831–2850. https://doi.org/10.1007/s10530-015-0914-3

Vallecillo, S., Brotons, L., & Thuiller, W. (2009). Dangers of predicting bird species distributions in response to land-cover changes. *Ecological Applications*, *19*(2), 538–549.

Vermeij, G. J. (1996). An agenda for invasion biology. *Biological Conservation*, *78*(1–2), 3–9. https://doi.org/10.1016/0006-3207(96)00013-4

Wan, H., Haye, T., Kenis, M., Nacambo, S., Xu, H., Zhang, F., & Li, H. (2014). Biology and natural enemies of *Cydalima perspectalis* in Asia: Is there biological control potential in Europe? *Journal of Applied Entomology*, *138*(10), 715–722. https://doi.org/10.1111/jen.12132

Wanger, T. C., Wielgoss, A. C., Motzke, I., Clough, Y., Brook, B. W., Sodhi, N. S., & Tscharntke, T. (2011). Endemic predators , invasive prey and native diversity. *Proceedings of the Royal Society B: Biological Sciences*, (September 2010), 690–694. https://doi.org/10.1098/rspb.2010.1512

Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., & Guisan, A. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

Zhang, Z., Mammola, S., McLay, C. L., Capinha, C., & Yokota, M. (2020). To invade or not to invade? Exploring the niche-based processes underlying the failure of a biological invasion using the invasive Chinese mitten crab. *Science of the Total Environment*, *728*, 138815. https://doi.org/10.1016/j.scitotenv.2020.138815

Zhu, H., Wang, D., Wang, L., Fang, J., Sun, W., & Ren, B. (2014). Effects of altered precipitation on insect community composition and structure in a meadow steppe. *Ecological Entomology*, *39*(4), 453–461. https://doi.org/10.1111/een.12123

→03

CHAPTER 03

Anticipating *B. sempervirens* viability in front of *C. perspectalis* outbreaks, fire, and drought disturbances.

Quim Canelles
Núria Aquilué
Lluís Brotons

This chapter is under review
in *Science of the Total Environment*

Abstract

Forest ecosystems face an increasing pressure of insect pest outbreaks due to changes in land-use, new climatic conditions, and the arrival of new invasive species. Also, insect outbreaks may interact with other shifting disturbances such as fire and drought, that eventually may boost the impacts of pests on forest ecosystems. In the case of invasive species, the lack of long-term data and their rapid spread challenges their study and require appropriate new management strategies to cope with them. Here we studied the case of boxwoods (*Buxus sempervirens*) in Southern Pyrenees under the pressure of the invasive insect box tree moth (*Cydalima perspectalis*), fire, and drought events. We projected the future of boxwoods through the development of a spatially explicit simulation model and its implementation under different climatic and ecological scenarios. The results showed an initial boxwood decay due to *C. perspectalis* fast spread but a later stabilization of the population resulting from a cyclic consumer-resources dynamic. Climate change is expected to reduce overall insect habitat suitability and future negative impacts on boxwoods. Furthermore, boxwood drought-induced mortality and burning will increase under new climatic conditions. Interaction between drought and insect pest conditioning regeneration after defoliation were negligible in our analyses. Boxwood decay was anticipated to be more notorious in locations under 800 m a.s.l. and in habitats where the species dominates the forest understory, while boxwood in open shrub forest types typical of higher elevations will be less endangered. Our results provide valuable information for boxwood and *C. perspectalis* management in a context of joint disturbance impacts and contribute to a better identification of the role of forest disturbances and their interactions.

KEYWORDS
Simulation model, landscape dynamics, invasive alien species, forest insect pest.

CHAPTER 03

Climate change is expected to reduce *C. perspectalis* habitat suitability and defoliation on boxwoods, but to increase wildfires and boxwood drought-induced mortaility.

Introduction

Natural disturbances play an essential role in forest ecosystem functioning and are key drivers of landscape changes (Seidl et al. 2017). Disturbance regimes have been shifting during the last decades worldwide because of anthropogenic pressure and the resulting global change (Dale et al. 2001; Turner 2010; Ayres and Lombardero 2018). For instance, forest pests are important agents of forest landscape change, shaping forest composition and structure, altering ecosystem functioning, and causing large economic impacts in both managed and planted forests (Hulme 2009; Turner 2010; Suárez-Muñoz et al. 2019). Such impacts have increased in the recent decades due to global change, as new climatic conditions alter insect development, reproduction, and population dynamics (Ayres and Lombardero 2000; Kingsolver et al. 2011), and changes in land-uses influence insect population distributions and local viability (Rosenberger et al. 2017). In addition, international trade has favored the introduction of invasive species into new ecosystems (Hulme 2009; Bradshaw et al. 2016). Invasive species spread and impact is boosted by climate change as many of them share traits such as short generation times, rapid dispersal or environmental plasticity that could be advantageous in a transitioning climate (Dukes and Mooney 1999). However, new climate conditions do not always lead to increasing the climatic niche of alien species, as each species could perform differently in distinct areas (Peterson et al. 2008; Bebber et al. 2013; Bates et al. 2020). For all this, the dynamics of invasive insect pests and their impact on ecosystems in a context of global change is a key factor when studying landscape dynamics and ecosystem viability (Fares et al. 2015; Suárez-Muñoz et al. 2019).

Other natural disturbances such as wildfires and drought events have been widely studied in their role of forest dynamics drivers (Silva et al. 2011; Williams et al. 2013). Land-use changes, new climate conditions, and disturbance management strategies have been described to push new forest disturbances regimes (Duane et al. 2019b). Furthermore, such background disturbances may interact with insect pests, drawing a complex diagram of synergistic and antagonistic relations that will ultimately impact on forests (Canelles et al. 2021a). For instance, drought may weaken the defensive system and recovery capacity of host plants (Sangüesa-Barreda et al. 2015; Wong and Daniels 2017), or insect pests may alter fuel load and thus, fire risk (Meigs et al. 2016).

The study of invasive insect pests impacts on forests and their interactions with other disturbances is usually challenging due to the limitations on obtaining long-term quality data and therefore, forecasting their dynamics under novel environmental conditions. In this context, landscape dynamics simulation models are useful tools to integrate disturbances available information into spatially explicit modelling frameworks, and to anticipate medium and long-term disturbance dynamics via projections under future global change scenarios (Keane et al. 2004, 2015; Gustafson et al. 2010). The ability of such simulation models to explore dynamics to distant futures is crucial in the case of insect pest disturbances because of the long-term spatial legacies they may create and the host-insect cyclic dynamics they may induce (Robert et al. 2020). Also, such modelling frameworks allow to test the relevance of certain processes and the weight of key parameters that are difficult to empirically estimate, but that may have a significant incidence in landscape dynamics (e.g., timing in disturbance processes, interactions between disturbances, etc.; Bouchard et al., 2019).

The case of box tree (*Buxus sempervirens* L.) in Southern Pyrenees (Spain) is a prime example to study the coexistence between insect pest, fire, and drought disturbances. *B. sempervirens* is the main undercover species in some mountain and temperate ecosystems in Southern and West Europe (Decocq et al. 2004; Di Domenico et al. 2012). Since 2007, the species deals with the invasive box tree moth (*Cydalima perspectalis* W.), native from Asia and introduced in Germany via the trade of ornamental box trees (Maruyama and Shinkaji 1987; Leuthardt 2013). Since then, the box tree moth has spread across Europe and has arrived up to Asia Minor (Nacambo et al. 2014; Bras et al. 2019). During its caterpillar phase, *C. perspectalis* feeds on species of the genus *Buxus* (only *B. sempervirens* in Europe), often leading to complete defoliation and dead of the host plant. Although the resprouting ability of boxwood plants, their survival capacity after few consecutive defoliation episodes is still unknown (Artola 2019). Distribution and impact of the box tree moth seems to be restricted by the presence of its host plant and by climate, that influence the diapause and larval development (Nacambo et al. 2014; Canelles et al. 2021b). Climate suitability for *C. perspectalis* is controlled by low precipitation seasonality and minimum annual temperatures around 0° C, limiting its climatic niche to Western Europe and coastal areas (Nacambo et al. 2014; Poitou et al. 2020; Canelles et al. 2021b). However, many other features of the ecology and potential impacts of the box tree moth are still unknown, such as the interaction with other competitors and predator species, possible host-pest cycling patterns, or the long-term effects to the invaded landscape.

Although effects of wildfires on *B. sempervirens* have not been widely studied, available evidence suggests that the species can resprout after fire, even if its viability and vigor after fire are conditioned by light availability, the age of individuals prior to fire, and the intensity of the fire disturbance itself (Casals and Rios 2018; Monfort-Bague et al. 2020). With respect to climate, *B. sempervirens* is an evergreen small-tree species, highly capable to cope with adverse weather conditions (like extreme temperatures or episodes of severe drought; Hormaetxe et al., 2007). However, some physiological experiments indicate that boxwoods are sensitive to persistent water stress conditions, and therefore it experiences leaves curling, shrinking, and decoloring, opening of the plant's canopy, and sagging of the branches that may lead to the dead of the plant (De Jong et al. 2012). In the European Mediterranean bioclimatic zone, the species is currently found where climate conditions are particularly stable with respect to water availability, such as wet fluvial valleys, gorges, ravines, and around mountain basins, indicating that water availability has a strong ecological influence on the distribution of the species and that aridification may compromise its viability (Di Domenico et al. 2012).

We aimed at studying the viability of *B. sempervirens* in Southern Pyrenees in a context of increasing *C. perspectalis* pest, fire, and drought impacts. In 2014, the tree box moth was first identified in the Spanish Pyrenees (Bassols and Oliveras 2014) and in 2017 a high severe impact to boxwood trees expanded through the east of the region covering up to more than 1500 km2. In addition, in this anthropized forest landscape, wildfires represent an important natural forest disturbance (Trabaud 1994; Duane et al. 2019a) and drought is projected to diminish tree growth and viability of tree species in their southern xeric distribution limits, as is the case of boxwood (Camarero et al. 2011; Gazol et al. 2020). Thus, ecosystems dominated by *B. sempervirens* are endangered in the area and to anticipate their viability is required to design adequate management strategies. We build a landscape dynamics simulation model to address the following questions: (1) What is the future viability of *B. sempervirens* according to its main disturbances? (2) What is the role of climate change on *B. sempervirens* disturbances and their dynamics? (3) Are these disturbances influenced by any spatial pattern and/or ecological variable (e.g., elevation, forest community)?

Methods

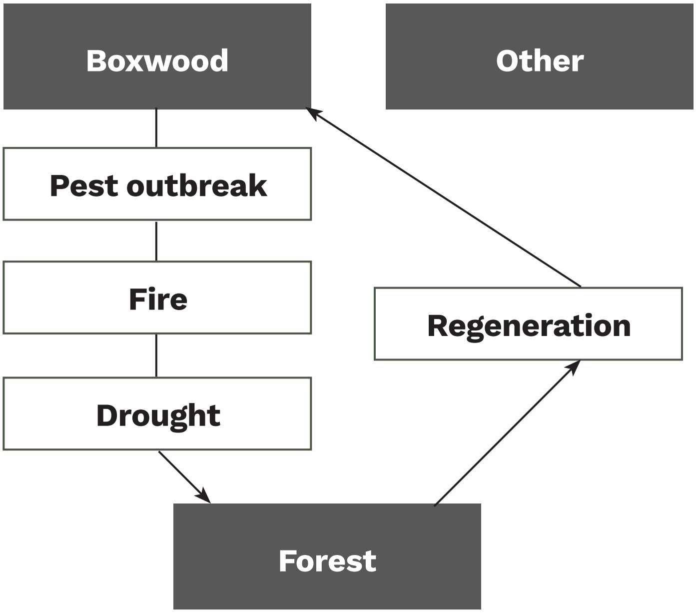
STUDY AREA

The area of study was the Spanish Southern Pyrenees (FIG . 1), which includes the regions of Catalonia, northern Aragon (Zaragoza and Huesca provinces), Navarra, La Rioja, and Basque Country. This area located in north-eastern Spain sums 87,684 km2. Its complex orography, with altitudes ranging from 0 to more than 3,000 m above sea level (a.s.l.), and coast lines extending over 970 km summing up the Mediterranean and Cantabrian coasts resulted in highly diverse climate and plant communities. The region is extensively covered by forest and scrublands (58%), while agricultural lands (36%) and urban areas (6%) contribute to the fragmentation of natural areas (*Spanish Forest Map*; Ministerio para la Transición Ecológica, 2013; Ibàñez et al., 2002). Forests are dominated by Aleppo pine (*Pinus halepensis* M.), Holm oak (*Quercus ilex* L.), Scots pine (*Pinus sylvestris* L.), and European black pine (*Pinus nigra* subsp. *salzmannii* A.), which together represent two thirds of the total forest surface. *B. sempervirens* is widely distributed in the study area, being essential for some of the ecosystem understory but also frequent in open shrubby areas. It is usually found in limestone of sub-Mediterranean environments, between 500 - 1,500 m a.s.l., although it can also be found in subalpine forests covering a range of 100 - 2,400 m a.s.l. (Folch, 1985).

MODEL OVERVIEW

In the modelling framework we developed, boxwood dynamics are driven by insect pest defoliation (*C. perspectalis*), fire, and drought, and can regenerate after several years without any type of these disturbance (FIG . 2). In this spatially explicit stochastic model, the spatial information is represented in raster format and covers the full extent of the study area at 1 km resolution. The temporal scale is fixed at one year and simulations are run from 2020 to 2080. The state variables whose values change because of spatial processes are land cover types (LCT; TABLE 1), time since last pest (TSP), and time since last fire (TSF). Climatic variables and consequently, climatic suitability for the boxwood and *C. perspectalis* species (SDMBuxus and SDMCyd, respectively) are annually updated with climatic niche data a priori calculated. Finally, fire risk is a static spatial variable that accounts for both fire ignition risk and fire spread probability (FireRisk).

▶ **FIGURE 1**
Location of the study area in the European context and provinces included in the Southern Pyrenees (Spain).



▶ **FIGURE 2**
Conceptual diagram of the simulation model. Land cover type differentiates Forest, Boxwood and Other. Pest outbreak, fire, and drought transform boxwood to forest, while boxwood re-establish after the regeneration process.

The model is implemented in R 3.6.1 (R Core Team, 2019) and available at GitHub (https://github.com/quimcanellestrabal/SM-Buxus-Cydalima/blob/main/Functions_scenarios_SimulationModel).

INITIAL CONDITIONS

Initial LCT differentiated three land cover types: forested areas without boxwood, including forests and shrublands (hereinafter "forest"); forested areas with boxwood, including forests and shrublands (hereinafter "boxwood"); and other land uses, including urban, water and crops (hereinafter "other"; FIG. 2). LCT layer was based on the *Spanish Forest Map* (Ministerio para la Transición Ecológica, 2013). Initial boxwood distribution was calibrated with information from National Forest Inventories (IFN; Villanueva, 2005), the *Map of Habitats of Catalonia* (Carreras 2004; Carreras et al. 2014), and the Global Biodiversity Information Facility (GBIF, 2019a).

Initial *C. perspectalis* distribution was estimated using species occurrence information from GBIF (GBIF, 2019b), the community science project Alerta Forestal (a collaborative tool where users upload field observation of forest disturbances; http://www.alertaforestal.com/es/), and observations obtained from forest rangers (Agents Rurals de la Generalitat de Catalunya). The initial distribution described 2019 state. To calibrate TSP, we gathered species occurrence from 2017, when the first severe impact of *C. perspectalis* was observed in the region (Artola 2019) to 2019. Initial TSF values for the period 2010–2019 were calculated based on wildfire patterns and fire historical statistics in the region (Ministerio de Agricultura Pesca Alimentación y Medio Ambiente., 2019).

DESIGN CONCEPTS

Pest

Boxwoods affected by *C. perspectalis* may die after severe pest episodes. In this study, box tree moth dynamics are based on species distribution models (Guisan et al. 2017) already generated by Canelles et al. (2021b). SDM for *C. perspectalis* (SDMCyd; TABLE 1) was calibrated with the species occurrence data (GBIF, 2019b) and climatic data from BIOCLIM (Fick and Hijmans 2017; Petrie et al. 2021) and Chelsa (Karger et al. 2017) for the period 1979-2013. SDMCyd was projected to the future for three periods (2021-2040, 2041-2060, and 2061-2080), but to overcome sudden changes in SDMCyd projections, annual variation in SDMCyd were calculated to derive a series of 1-year SDMCyd data.

We differentiated *C. perspectalis* distribution (where the species is present) from severity (measured as extensive defoliation leading to boxwood dieback). Species distribution depended on the distance to species occurrences in the year before (MaxCydDist; 5 km according to Canelles et al. (2021b), a climatic suitability threshold for *C. perspectalis* occurrence (ThCyd; calibrated with the mean value of the SDMCyd in the percentile 5 of all species observations), and a random factor weighted by SDMCyd value (the higher SDMCyd value, the more probability to pest occurrence).

Boxwood died after severe pest defoliation episodes and the LCT variable changed to forest. Levels of severity depended on the number of consecutive years of *C. perspectalis* occurrence (CydIncidence; a model parameter that changes according to the scenario), a climatic suitability threshold for pest severity (ThCydSev; calibrated by overlapping the SDMCyd data and high defoliation observations according to Agents Rurals de la Generalitat de Catalunya and Alerta Forestal), and a random factor weighted by a SDMCyd value (the higher SDMCyd value, the more probability to severe pest attack).

Fire

Fire disturbance may burn both forest and boxwood areas, but not other land covers. All pixels (either boxwood or forest) become forest after burning. Pixels with TSF equal or lower than 10 years were assumed to lack the required amount of fuel and cannot burn (MinTSF; TABLE 1). Number and sizes of fires were derived from the projections used in Duane, et al., (2019a). Fire ignition and spread were simulated using the *SpaDES* R package (Chubaty & McIntire, 2021), and both probabilities depend on a fire risk map calibrated according to elevation, aspect, and slope (FireRisk; Burriel, 2017).

PARAMETER	**DESCRIPTION**	**VALUE**	**DATA SOURCES**
Land Cover Type (LCT)	State variable layer. It is dynamic because of the model processes.	3 categories: boxwood, forest, and other	Spanish Forest Map, National Forest Inventory, Map of Habitats of Catalonia, Global Biodiversity Information Facility.
Time Since Pest (TSP)	State variable layer. It is dynamic because of the model processes.	Numeric (years)	Global Biodiversity Information Facility, Alerta Forestal, Agents Rurals de la Generalitat de Catalunya
Time Since Fire (TSF)	State variable layer. It is dynamic because of the model processes.	Numeric (years)	Generalitat de Catalunya; Ministerio de agricultura, pesca y alimentación
FireRisk	Ignition and spread probability. State variable layer.	Numeric (index between 0-1)	Burriel, 2017
Initial *Cydalima* distribution	Presence spatial points.		Global Biodiversity Information Facility, Alerta Forestal, Agents Rurals de la Generalitat de Catalunya
SDMCyd and its projections	Suitability index for *C. perpsectalis.* Variable layer. It is dynamic because the information is external to the model.	Numeric (index between 0-1)	Canelles et al., 2021b
MaxCydDist	Annual flight distance by *C. perspectalis.* Fixed value	5 km	Canelles et al., 2021b
ThCyd	Threshold that determines the pest occurrence. Fixed value.	Numeric	Mean value of the SDMCyd in the percentile 5 of all species observations according to Alerta Forestal and Agents Rurals de la Generalitat de Catalunya.
CydIncidence	Consecutive years of pest occurrence to generate severe impact.	Numeric (years)	According to the scenario.

PARAMETER	**DESCRIPTION**	**VALUE**	**DATA SOURCES**
ThCydSev	Threshold that determines the severe pest. Fixed value.	Numeric	Mean value of the SDMCyd in the high severity points according to Alerta Forestal and Agents Rurals de la Generalitat de Catalunya.
MinTSF	Consecutive years without fire to burn again. Fixed value.	10 years	Brotons et al., 2013
Fire number and size distribution	Table with fixed values.	Number of fires is numeric. Size of fires has 6 categories: 1, 3, 5, 10, 100, 500 km2	Duane, et al., 2019a
SDMBuxus and projections	Suitability index for *B. sempervirens*. Variable layer. It is dynamic because the information is external to the model.	Numeric (index between 0-1)	Calculated with GBIF occurrences and BIOCLIM and CHELSA climate data.
ThBuxus	Threshold that determines the effect of drought. Fixed value.	0.45	Mean SDMBuxus value of the boxwoods in the lowest percentile 5.
ThBuxusReg	Threshold that determines the regeneration. Fixed value.	0.83	Mean SDMBuxus value of the boxwoods in the highest percentile 50 / According to the scenario.
Time since pest for regeneration (TSPReg)	Consecutive years without pest to regenerate. Fixed value.	Numeric (years)	According to the scenario.

▶ **TABLE 1**
Name, description, value, and source of the parameters used in this study.

Drought

Boxwoods may die because of water availability constraints (i.e., drought). Here, boxwood sensitivity to drought was estimated using climatic SDM for the boxwood species (SDMBuxus; TABLE 1). SDMBuxus was calibrated with data from all Europe using occurrences of the species from GBIF, 10,000 randomly generated background points across the species distribution extent (Ellith 2011, Phillips 2009), and climate information from BIOCLIM (Fick and Hijmans 2017; Petrie et al. 2021) and Chelsa (Karger et al. 2017) for the period 1979-2013. Climate variables included isothermality, maximum temperature of warmest month, minimum temperature of coldest month, mean temperature of wettest quarter, mean temperature of driest quarter, annual precipitation, and precipitation seasonality (bio3, bio5, bio6, bio8, bio9, bio12, and bio15, respectively according to BIOCLIM code). These variables were the final selection from an initial set of 19 climate variables that were subjected to a multicollinearity test using Pearson's correlation coefficient and variance inflation factor analysis (Marquaridt 1970). We finally selected only one variable from each set of highly correlated variables ($|r| > 0.7$; $VIF > 10$) depending on its relative contribution to the overall model. SDMBuxus was assembled by the species distribution modeling algorithm MaxEnt in R 3.6.1 (R Core Team, 2019) with the *dismo* package (Hijmans, 2017). We realized a sample data-splitting procedure to evaluate the models. First, models were calibrated with 70% of the initial data. Second, models were run 10 times taking the average as the final model. Finally, models were evaluated on the remaining 30% of initial data with two model evaluations: the area under the receiver operating characteristic curve (AUC; Hanley and McNeil, 1982) and the continuous Boyce index (CBI; Boyce et al., 2002). SDMBuxus was projected to the future with climatic data for the periods 2021-2040, 2041-2060, and 2061-2080. To overcome sudden changes in SDMBuxus projections, the annual SDMBuxus variations were calculated to derive a series of 1-year SDMBuxus data. We defined a climatic suitability threshold (ThBuxus, TABLE 1) to identify the boxwoods that were under a persistent drought situation and may die. Such threshold value is calculated as the mean SDMBuxus value of the boxwoods in the lowest percentile 5. However, this threshold value was initially lower and annually increased the first 10 years to avoid an imbalance of dead by drought the first year.

Regeneration

Regeneration of boxwood is the process of forest shift into boxwood. This happens in locations where boxwood was present at some point in the past, TSF is higher than 10 years or TSP is higher than the minimum time since pest needed to regenerate (TSPReg; this value changed according to the scenario; TABLE 1), and SDMBuxus is higher than a threshold value (ThBuxusReg). This threshold is calculated as the mean SDMBuxus value of the boxwoods in the highest percentile 50.

Scenarios

We designed two sets of scenarios to explore the role of climate and *B. sempervirens* ecology respectively, on the viability of the species at the landscape scale in the future (TABLE 2). First, we tested the effect of climate on boxwoods and the related disturbances. We therefore considered three future climatic conditions: no change (Business-As-Usual, ClimBAU), moderate climate change (ClimMOD), and severe climate change (ClimSEV). The climate change scenarios were framed within the Representative Concentration Pathways (RCPs) built for the assessment report on climate change IPCC5 (Moss et al., 2010). We used RCP 4.5 (for ClimMOD) and RCP 8.5 (for ClimSEV) for the periods 2021-2040, 2041-2060, and 2061-2080 (Karger et al. 2017; Petrie et al. 2021).

Second, although boxwood resprouts after defoliation, the capacity of doing so after some consecutive years of *C. perspectalis* attacks was still unknown. Furthermore, low climatic suitability may influence boxwood regeneration. Thus, we tested the implication in boxwood dynamics of climatic requirements in the regeneration process through the ThBuxusReg parameter (i.e., low ThBuxusReg value indicates that boxwood regeneration was not constrained by climate, meaning that drought and the other disturbances did not explicitly interact; ClimMOD_NoInt). Finally, we also analyzed boxwood regeneration dynamics according to the number of consecutive years of *C. perspectalis* defoliation considered to be a severe outbreak (CydIncidence) and the minimum time to regenerate (TSPReg) in a new scenario named ClimMOD_ShortInc. We ran these two last scenarios under RCP 4.5 climatic conditions and compared them with ClimMOD.

SCENARIO	**CLIMATE**	**ThBuxusReg**	**CydIncidence**	**TSPReg**	**DESCRIPTION**
ClimBAU	BAU	0.83	5	10	This scenario assumes that current climate will persist in the future.
ClimMOD	RCP 4.5	0.83	5	10	This scenario simulates that climate will change moderately as CO2 emissions peak around 2040 and then decline. We used this as the baseline scenario.
ClimSEV	RCP 8.5	0.83	5	10	This scenario simulates that climate will severely change as CO2 emissions continue to rise.
ClimMOD_NoInt	RCP 4.5	0.45	5	10	This scenario simulates a moderate climatic change, and that climate does not constraint boxwood regeneration, meaning no interaction between drought and insect pest outbreaks or fire.
ClimMOD_ShortInc	RCP 4.5	0.83	2	2	This scenario simulates a moderate climatic change and that boxwood dies after only two consecutive years of severe pest defoliation, but regeneration occurs after a short time period.

▶ **TABLE 2**
Description and parametrization of the scenarios.

Analysis
We ran 30 simulation replicates of each scenario from 2020 to 2080 at 1-year time step. Response variables were annual occurrence of severe pest defoliation, fire, drought, and boxwood regeneration. Based on these variables we further analyzed the trend of boxwood occurrence and the dynamics of the three main disturbances considered, the total area affected by each disturbance by 2080, and their probability of occurrence at the cell-level. We explored the disturbance occurrence as function of elevation and forest type (differentiating open boxwood shrub areas with no canopy and forests where boxwood dominates the understory; Ministerio para la Transición Ecológica, 2013; Carreras, 2004). All analysis were fitted using the *glm* function in R (R Core Team 2019) and significance level was considered at *p-value* < 0.05. Finally, we evaluated the regional distribution of boxwood disturbances (i.e., administrative division by provinces).

Results

BOXWOOD DYNAMICS ACCORDING TO FOREST DISTURBANCES

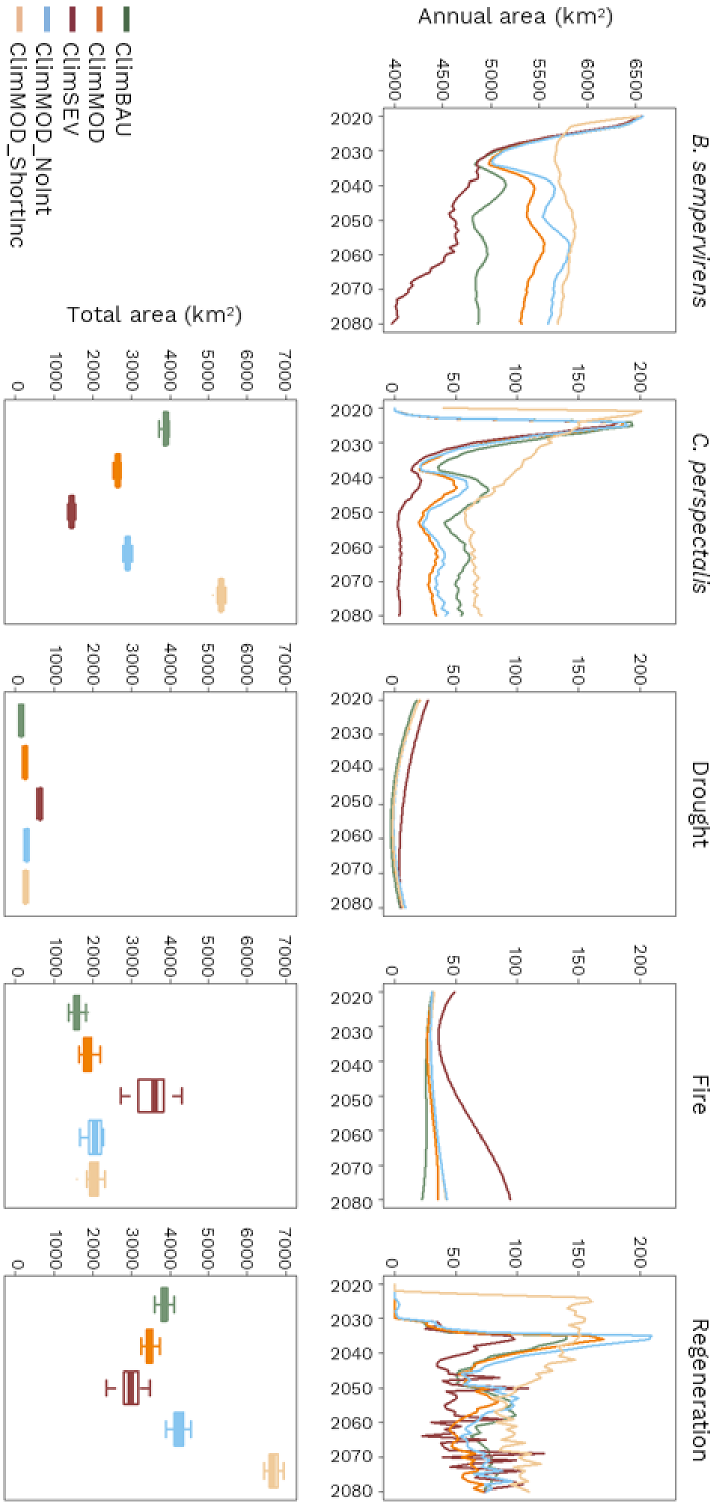
Viability of *B. sempervirens* in Southern Pyrenees is under the pressure of drought, wildfires, and insect pest outbreaks. According to our model, the area of distribution of the species decayed during the initial period 2020-2035 (13% – 30% of area loss according to the scenarios). After that, a cyclical dynamic was predicted, defining a general trend of boxwood area loss by 2080 up to 14 – 40% of the initial area, as anticipated by the different scenarios (FIG. 3).

C. perspectalis severe impact appeared as the disturbance that most largely affected boxwoods. In all scenarios, *C. perspectalis* dynamics experienced an initial (2020- 2025) expansion of its distribution area reaching 23% of the boxwood area and consequent boxwood severe defoliation (3% of the boxwood area), a decay of its distribution between the period 2025-2035, and it followed a cyclic consumer-resources pattern that tended to stabilize. After 60 years of simulation, scenarios varied between 21.000 and 58.000 km2 of *C. perspectalis* total area of distribution, and between 1.400 and 5.400 km2 of area severely defoliated (ClimSEV and ClimMOD_ShortInc, respectively in both cases).

Wildfires represented annual losses of boxwood of 20 – 50 km2 (less than 1% of the boxwood area) and by the end of the simulation, total burned boxwood area ranged between 1.500 and 3.800 km2 (ClimBAU and ClimSEV, respectively). *B. sempervirens* mortality by drought was not negligible and compromised between 2 – 9% of the boxwood area by the year 2080 (in ClimMOD and ClimSEV where climate change was simulated; TABLE 2). Drought-induced mortality was more pronounced between 2020 – 2050 than 2051 – 2080, being consistent with the climatic niche future projections (see Supplementary FIG. 1).

Boxwood regeneration started after the time considered by TSPReg (2 or 10 years according to the scenarios) and its dynamics was linked to *C. perspectalis* severe attack. From the first peak of regeneration, regeneration occurred to a maximum of 3% of the boxwood area, representing a sine wave according to the consumer-resources dynamics described above. By the end of the simulation, total boxwood regenerated area was 3.000 – 6.800 km2 (ClimSEV and ClimMOD_ShortInc, respectively).

▶ FIGURE 3
Distribution area of *B. sempervirens*, area affected by *C.perspectalis* outbreaks, drought, and wildfires, and area of regenerated boxwood under the five scenarios considered (TABLE 2), both in annual dynamics from 2020 to 2080 (upper row) and total area affected by the end of the simulation (lower row). Drought and fire annual dynamics are simplified to their trends (exponent 3) to facilitate their comprehension.


B. sempervirens
C. perspectalis
Drought
Fire
Regeneration
Annual area (km²)
Total area (km²)
4000
4500
5000
5500
6000
6500
0
50
100
150
200
1000
2000
3000
4000
5000
6000
7000
2020
2030
2040
2050
2060
2070
2080
ClimBAU
ClimMOD
ClimSEV
ClimMOD_NoInt
ClimMOD_ShortInc

THE ROLE OF CLIMATE CHANGE

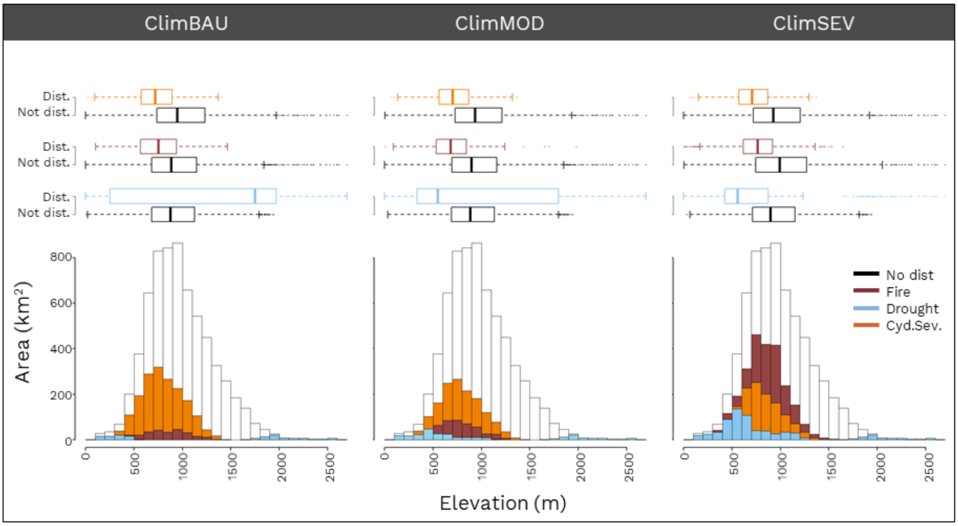
Climate strongly constrained *C. perspectalis* spread and derived severe impacts on boxwoods (Supplementary FIG. 2). *C. perspectalis* habitat suitability decreased under climatic change projections, translating into a decreasing trend of the distribution and impact of the pest, a less pronounced cyclability, and a lower total area of distribution and severe impact (FIG. 3).

The dynamics of severe impact caused by *C. perspectalis* showed higher values of defoliation under BAU climatic conditions (ClimBAU), leading a trend to up to 60 km2 of annual defoliation. Under RCP 4.5 conditions (ClimMOD), the annual affectation was up to 30 km2, and close to 0 km2 under RCP 8.5 projections (ClimSEV). This implied significantly different total area affected by the insect by the end of the simulation: higher in ClimBAU (3.950 km2), then ClimMOD (2.730 km2), and the lowest in ClimSEV (1.300 km2; *p-value* < 0.001 in all cases; FIG. 3).

Boxwood mortality by wildfires and drought increased under climatic change conditions. By 2080, total area of drought-induced mortality was significantly higher under RCP 8.5 conditions (630 km2), followed by those scenarios under RCP 4.5 conditions (270 km2), and lower under BAU conditions (160 km2; *p-value* < 0.001 in all cases; FIG. 3). Total area burned (of forest and boxwoods) was also lower under BAU conditions than under climatic change scenarios because of the input fire information (Duane, et al., 2019a; FIG. 3). Finally, and as a consequence of the dynamics described above, by the end of the simulation boxwood total area was higher in ClimMOD (5314 km2), followed by ClimBAU (4870 km2) and lower in ClimSEV (5314 km2; *p-value* < 0.001 in all cases; FIG. 3).

SENSITIVITY TO PARAMETRIZATION

When omitting climate constrains for boxwood regeneration (ClimMOD_NoInt), trends of *C. perpsectalis* severe impacts and boxwood regeneration were similar than when considering such climate requirements (ClimMOD). However, regeneration and insect defoliation in ClimMOD_NoInt were slightly higher every year, leading to a final total defoliated and regenerated areas significantly higher than in ClimMOD (2908 km2 and 4233 km2, respectively; *p-value* < 0.001 in both cases; FIG. 3). The effect of other disturbances was not significantly different between



▶ FIGURE 4

Asynchrony between *B. sempervirens* and the disturbances distributions according to elevation. Histograms show the area of disturbed vs. not disturbed boxwoods according to the elevation. Boxplots indicate the differences in elevation between disturbed and not disturbed boxwood.

ClimMOD and ClimMOD_NoInt neither in the dynamics trend or the total area affected (*p-value* = 0.79 in the case of fire; *p-value* = 0.26 in the case of drought). Lastly, final boxwood area in 2080 was higher in ClimMOD_NoInt than ClimMOD (5595 km2; *p-value* < 0.001; FIG. 3).

When the boxwoods died after only two consecutive years of pest severe defoliation and regenerated after two years (ClimMOD_ShortInc), the period of the insect pest – boxwood cyclability was shorter than in the other scenarios. Consequently, dynamics of *C. perspectalis* severe impact and boxwood regeneration influenced more area annually in ClimMOD_ShortInc than in ClimMOD, and the total area affected by *C. perpsectalis* severe impact and regeneration were significantly higher in ClimMOD_ShortInc (5322 km2 and 6647 km2, respectively; *p-value* < 0.001 in all cases). However, wildfires and drought were not different between ClimMOD_ShortInc and ClimMOD in their dynamics, neither the total area affected (*p-value* = 0.26 and *p-value* = 0.52, respectively). Final boxwood area in 2080 was higher in ClimMOD_ShortInc than in ClimMOD (5694 km2; *p-value* < 0.001; FIG. 3).

THE ROLE OF ALTITUDE AND HABITAT

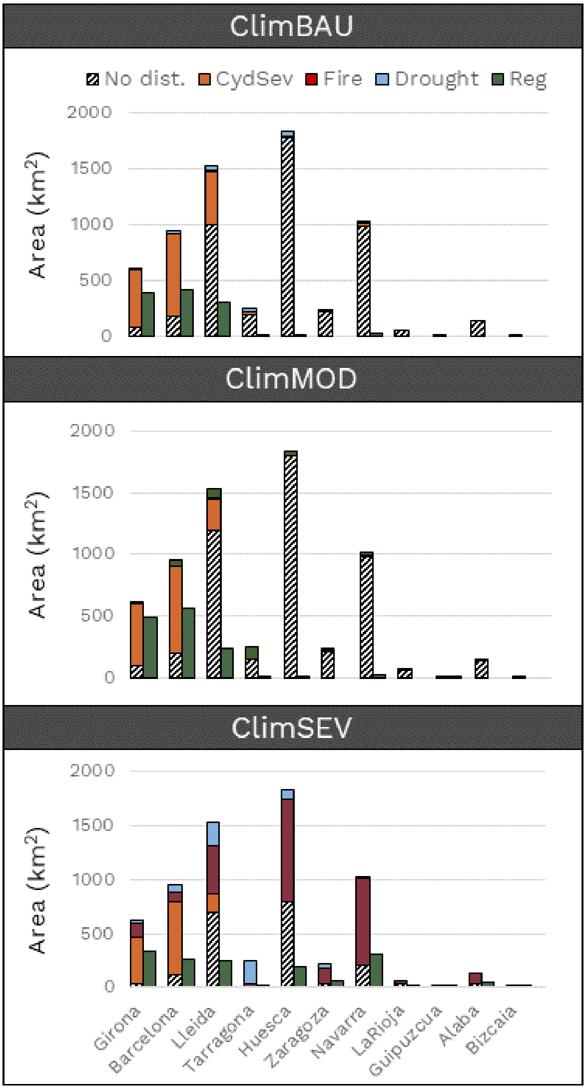
Our analyses showed that *C. perspectalis* severe defoliation was more likely at lower elevations (between 500 - 1100 m a.s.l.) than at higher elevations (*p-value* < 0.001 in all scenarios; FIG . 4). A similar pattern was found in wildfire distribution, that mostly burned forests and boxwoods below 1000 m (*p-value* < 0.001 in all scenarios). Drought-induced mortality occurred in both lower and upper limits of the boxwood altitudinal distribution (*p-value* < 0.001 in all scenarios). In scenarios with climate change, more boxwood died in the lower elevation range than in the upper (FIG. 4). Because of the incidence of the three disturbances, elevation factor was significant when analyzing the total disturbance probability, being boxwoods at lower elevations the most endangered (*p-value* < 0.001 in all scenarios).

Analyses of forest type in which boxwood is most commonly found revealed that open boxwood shrub areas were less probably affected by *C. perspectalis* and drought than boxwoods found in forest understories (*p-value* < 0.001 in both cases in all scenarios). However, both forest types were equally affected by wildfires (*p-value* > 0.2 in all scenarios).

SPATIAL PATTERNS IN DISTURBANCE EFFECTS

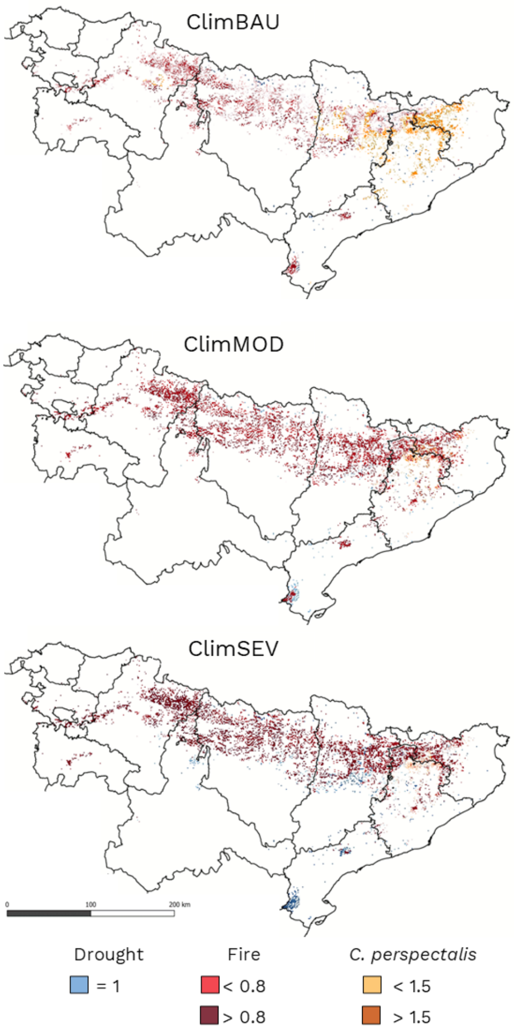
Boxwood distribution in the Spanish provinces of the Southern Pyrenees is unequal (FIG S. 5 AND 6): Huesca, Lleida, and Navarra host more than 1.000 km2 of boxwood distribution each; Barcelona, Girona, Tarragona, Zaragoza, and Alaba between 100 and 1.000 km2 and, La Rioja, Guipuzkua and Bizkaia have less than 100 km2 of boxwood. According to our simulations, the viability of boxwood and the impact of each disturbance was also different in each province and scenario. While boxwood viability was higher in the provinces of Huesca, Navarra, Zaragoza and La Rioja, populations in Barcelona and Girona were severely threatened (only 13-21% and 5-15% of all boxwood without any disturbance according to the scenario, respectively; FIGS. 5 AND 6).

Defoliation by *C. perspectalis* was the main disturbance in Girona (68% – 84% of all boxwood according to the scenario; FIG. 5), Barcelona (70% – 78%), and Lleida (11% – 38%). Most of the boxwood in these regions were affected by the insect, but also showed high regeneration indexes. In the provinces of Navarra, Tarragona, and Huesca *C. perspectalis* was testimonial, and completely absent in the other regions.



▶ **FIGURE 5**
Boxwood area affected by *C. perspectalis*, wildfires, and drought, as well as regenerated area in every province from east to west according to different scenarios.

Wildfires burned boxwood formations differently according to the climate scenarios. Under BAU climatic conditions, wildfires were not a relevant disturbance for boxwoods in any region, but it was under climate change. Under a moderate emissions scenario, wildfires were the main disturbance in Zaragoza (7% of all boxwood), Navarra (6%), and Huesca (4%), while under a higher emissions scenario, wildfires represented a major endangerment for boxwoods all over the territory, mainly in Navarra (80%), Zaragoza (68%), Huesca (52%), La Rioja (52%), Lleida (30%), and Girona (22%). Finally, drought was more severe in the regions of Tarragona (10% – 80% according to the scenario), Zaragoza (1% – 20%), and Lleida (3% – 13%). Drought impact was more notorious in those scenarios with climate change (FIG. 5).



▶ FIGURE 6
Recurrence of boxwood disturbances (average of times across all the model replicates)during the period 2020-2080 for the three climatic scenarios.

Discussion

Here we studied boxwood viability in Southern Pyrenees under the combined pressure of three different forest drivers. The invasive insect species *C. perspectalis* strongly impacts boxwood in eastern, more humid regions of the study area (Girona and Barcelona provinces). Wildfires are also predicted to be a major disturbance for all boxwood formations, while drought-induced mortality seems to be less harmful across the study area. However, climate change influences all these dynamics: it leads to an increase of the drought pressure and the burned area per year, but it may strongly constraint the expansion and severity of the impact caused by the box tree moth. These dynamics compromise boxwood viability in the future and should be considered to manage these forest ecosystems.

ANTICIPATING *C. PERSPECTALIS* EXPANSIONS

Biological invasions follow these consecutive phases: (a) arrival, (b) establishment, (c) dispersion, and (d) impact (Vermeij 1996; Sakai et al. 2001; Blackburn et al. 2011). In the case of *C. perspectalis*, it arrived in Southern Pyrenees in 2014 in Girona. The species established in this region and further dispersed throughout the territory. According to the population dynamics here simulated, the species is still in the phase of dispersal, and it will likely reach its maximum distribution around 2025, while the effects on boxwood populations will become more noticeable in those areas with consecutive years of defoliation.

After the spreading peak, our models predicted a cyclic pattern both for the *C. perspectalis* populations and the outbreak severity. This pattern is broadly described in animal populations, in Lepidoptera order in particular (Myers 1988; Allstadt et al. 2013; Myers and Cory 2013; Tenow et al. 2013), and found in forest pests like *Lymantria dispar* L. (Allstadt et al. 2013), *Operophtera brumata* L. (Tenow et al. 2013), or *Malacosoma disstria* H. (Cooke and Lorenzetti 2006). Such populations fluctuations can be motivated by several reasons including food limitation, induced plant defenses, pathogens incidence, parasitoids or predators, and patterns of fecundity (Myers 1988). In our model, the fluctuations of *C. perspecatlis* populations are directly caused by food limitation, following an extension of the Lotka-Volterra model that tightly links consumer (i.e., *C. perspectalis*) and resources (i.e., boxwood) dynamics (Vandermeer, 2006; Wilson et al., 2003). Cyclic population patterns are more evident in those scenarios without climate change where there are less ecological pressures on the insect (ClimBAU). Even so, *C. perspectalis* is an invasive species in the process of dispersion and not in equilibrium with the new habitat, so many other factors can influence these fluctuations either by emphasizing them (e.g., fertility patterns linked to population density, parasitism or predation relationships; Myers and Cory, 2013) or reducing them (e.g., new introductions in particular areas).

In spite of the overall fluctuating pattern simulated, *C. perspectalis* tends to a stabilization of its distribution and impact at around 12% and 1% of the initial boxwood extension, respectively. Such distribution and impact will be concentrated only in climate suitable areas and may lead to an isolation of the *C. perspectalis* populations in the near future.

THE ROLE OF CLIMATE CHANGE

Climate change influences the transport, distribution, and impact of invasive species (Hellmann et al. 2008). In the case of forest pests, changes in temperature may create favorable conditions for the species development and dispersal, leading to more severe disturbance impacts (Robinet and Roques 2010). However, new climate conditions do not always increase the climate niche of forest pest species and there are also examples of outbreaks that have been diminished due to climate change (Ims et al. 2008). Projections of *C. perspectalis* climatic suitability anticipated a regression of the favorable area in the future. This loss of climate niche was more remarkable under more severe climatic projections (higher distribution regression in RCP 8.5 conditions than in RCP 4.5). This result may seem counterintuitive at first sight since the increase in temperatures is usually associated with an increase in suitable conditions for *C. perspectalis* involving a possible movement of the species towards higher elevation areas. Likely, the moth may have better conditions for its development during a longer time, what implies more viable generations per year and a more subsequent severe impacts on boxwoods, as it happens with other pest species (Robinet et al. 2007). However, Myers & Cory, 2013 postulated that climate change leading to warmer temperatures may reduce the frequency of forest Lepidoptera outbreaks. In the case of *C. perspectalis*, Canelles, et al. (2021b) demonstrated that mild climate conditions including abundant precipitation with low seasonality and small temperature diurnal range are the optimal climatic conditions for the species. Thus, under future climate change, precipitation and temperature seasonality will increase as well as drought will to the detriment of *C. perspectalis*. The reduction in the climatic suitability was reflected in smoother fluctuations of the populations, and a tendency to low impact values, resulting a secondary disturbance for boxwoods across most of the territory (FIG. 3).

Several studies have predicted increases in wildfire activity to the end of the century in Mediterranean ecosystems (Amatulli et al. 2013; Batllori et al. 2013; Turco et al. 2018). It is not only an increase in the number of fires, but in the type and impact of these, since the new climatic conditions may lead to an increase in large wildfires (Duane et al. 2019a). In this study case, we projected how the total burned area and boxwood area could increase under climate change scenarios. Although these fires were unequally distributed across the territory, they represented the main pressure on boxwood populations in some scenarios. Here again, as the species has a great regeneration capacity post fire, it is described as a passive pyrophyte (Di Domenico et al. 2012). Recurrence and burning intensity of fire episodes both seem to be crucial for the species viability (Casals and Rios 2018).

B. sempervirens is classified as an evergreen shade and drought tolerant species (Niinemets and Valladares 2006). However, in the Mediterranean region, boxwoods suffer an aridification process that led to populations fragmentation and overall species decline (Di Domenico et al. 2012). In our modelling framework, we introduced the SDMbuxus parameter to study the climate suitability of boxwood in the area and the projected damage of adverse climatic conditions. Higher climatic suitability for boxwoods was found when maximum temperatures were between 10 and 20 °C, minimum temperatures were not lower than –5 °C, and annual precipitation was between 500 and 2.500 mm year-1, conditions mainly observed in mid mountain areas. However, our results showed that adverse climatic conditions were not a major disturbance for boxwoods, meaning only a small percentage of the general boxwood decline. Even under climate change conditions (both RCP 4.5 and RCP 8.5 scenarios) drought-induced mortality was not the main disturbance and only affected the populations in the limits of the climatic niche, found in particular locations and elevations (discussed below).

BOXWOOD REGENERATION AND ITS RELATIONSHIP WITH DROUGHT

Boxwood population in Southern Pyrenees is projected to suffer an important decay in the following years mainly due to the impact of *C. perspectalis* and wildfires. However, because its regeneration capacity and the reduction of the insect climatic niche, boxwood may recover, and its population stabilize (only under most severe climate change conditions boxwood decay will continue). Regeneration capability of boxwood is argued to be high enough to ensure the viability of the species under different disturbances pressures. Although it is described that boxwoods attain status as a mature plant about 10 years after being burnt (Casals and Rios 2018), it is still unknown whether the plant is capable to resprout after repetitive attacks of *C. perspectalis*, and the time needed to do so. In this study, we assumed that the box tree always regenerates after enough time without any kind of disturbance and the climatic conditions are favorable. We checked different timings for boxwood dead after pest outbreak and for regeneration via scenario parametrization. Results showed that regeneration is conditioned by the cyclability pattern of *C. perspectalis*. The period of fluctuation of the populations changed according to such parameterization (much shorter in ClimMOD_ShortInc) but the general trend of the boxwood and its moth populations was not different. Thus, regeneration has a decisive role in boxwood viability, but the time needed to regenerate does not affect the general dynamics of populations. However, a long-term data monitoring is required to confirm such patterns and the validation of these parameters.

Climate suitability requirements after defoliation were also reported to influence boxwood regeneration. Drought often interacts with insect outbreaks through hindering of insect performance, but also via changes in the suitability of the host species and its response capacity (Sangüesa-Barreda et al. 2015; Wong and Daniels 2017). In this study, we hypothesize that regeneration post-fire or post-pest may not occur under adverse climatic conditions for the host plant (Petrie et al. 2016; Casals and Rios 2018; Monfort-Bague et al. 2020). If only one of the disturbances acted (fire or insect pest) the boxwood could regenerate, but the combination of these disturbances with drought conditions may lead the species dieback. We used different scenarios to verify the effect of climatic requirements on regeneration capacity. Results showed that if boxwood regeneration was constrained by high climatic suitability, the cyclic waves of *C. perspectalis* and boxwood regeneration would be more pronounced. On the other hand, the trend of the host-pest dynamics was similar whether such the interaction with drought was considered or not. This means that such interaction was not relevant for the viability of boxwood neither the behavior of *C. perspectalis* populations.

There are other interactions to study in this context, as insect outbreaks have often complex relationships with other forest natural disturbances and can affect and be affected by fire and drought among others (Canelles et al. 2021a). For instance, the lack of boxwood in some understory forests because of insect defoliation may influence the fuel availability for subsequent fires (Meigs et al.

2016) or how fire weakens the defensive system of the host plant contributing to insect pest establishment (Kelsey and Joseph 2003; Lombardero and Ayres 2011). But these questions require specific information to be answered and are beyond the scope of the present study.

UNEVEN BOXWOOD VIABILITY

Boxwoods are mainly found in mountain systems, but also some scarce populations are placed in wet locations at low elevations that are reminiscences from the historical species distribution (Di Domenico et al. 2012). Conversely, other populations are found at higher elevations, in the limit of the treeline and, in some cases, in south faces of the mountain as is the case of Cadi range (Carreras 2004). In the study area, boxwoods were mainly distributed between 600 and 1.200 m a.s.l., however boxwood disturbances were concentrated between 600 and 800 m a.s.l, showing that elevation matters for the viability of the species (FIG. 4).

The SDMbuxus parameter defined climate suitability for the species in mid mountain system and those boxwood populations placed at higher elevations or in lowlands are more susceptible to die because of adverse climatic conditions. Fire probability is also directly related with elevation (Broncano and Retana 2004; Brotons et al. 2013) and our projections confirmed that fire affected more those forested areas at lower elevations. Finally, according to SDMCyd that restricted distribution and impact of *C. perspectalis*, climate suitability for the species was characterized by a certain continentality effect (being more suitable in the coast than inland) and defined lower climatic suitability at higher elevations (Canelles et al. 2021b). Thus, *C. perspectalis* impact was concentrated around 800 m a.s.l. and completely null over 1.400 m a.s.l. Because of the disturbance distribution, we argue that boxwoods present in the limit of its climate niche (in lowlands or over 1.800m a.s.l.) or around 800 m a.s.l. are the more susceptible to be damaged.

We also found uneven viability between the different hosting boxwood forest types. In the studied area, boxwoods are commonly found in open boxwood shrub areas from mid mountains limestones as a dominant species or coexisting with *Amelanchier ovalis* Nutt., *Rhamnus saxatilis* Jacq., and as understory species in forests of *Quercus ilex* L., *Q. pubescens* Willd., *Fagus sylvatica* L., *Pinus sylvestris* L., *P. nigra* J.F.A., *Abies alba* Mill., and *Fraxinus excelsior* L. (Carreras 2004). We showed that boxwoods in open shrub areas were less probably affected by *C. perspectalis* severe defoliation and drought than boxwoods in forest understory, so its viability was less compromised. We recognize that forest types also respond to elevation gradients, so such pattern may not be related to the microclimatic conditions or habitat dynamics of the different forest types but only to the elevation constrains to boxwood disturbances. However, we consider this result of enough value to apply correct management strategies in particular habitats.

Finally, we checked how disturbances were distributed across the Southern Pyrenees. Although boxwood was mainly present in Huesca, Lleida, Navarra, Barcelona, and Girona provinces (Supplementary FIG. 1), *C. perspectalis* impacts were concentrated in the last two. According to our projections, severe outbreak is already near its peak and, although the insect could still spread further, it does not seem that it will affect areas which have not already been affected. Provinces hosting small and residual boxwood populations may be lost because of drought, as anticipated to happen in Tarragona. Uneven distribution of boxwood viability compromises entire habitats and the age of boxwoods in some regions. Again, this should be considered by managers as well as by manufacturers of products derived from boxwood (Mitchell et al. 2018).

CHALLENGES IN BOXWOOD-*CYDALIMA* MANAGEMENT

Boxwood loss has cultural, economic, and ecological consequences. Ecologically, boxwoods host hundreds of fungi, chromists, lichens and invertebrate; indeed, 64 species are only found in this host plant (Mitchell et al. 2018). At the landscape scale, boxwoods represent a key species of different habitats and singular forests in the study area (Comas et al. 2013). Although boxwood is not an important forest species in terms of wood economy, it is valuable in gardening and there is a small market related with wood kitchen utensils. Also, boxwood loss could have major indirect and non-market economic effects, as forest recreation.

Since we showed that boxwood disturbances are and will still be concentrated in some regions and forest types, prioritizing management interventions considering its threats, its ecological relevance, and its economic value would be required (Mitchell et al. 2018). Such priorities may include mixed deciduous forests present in Tarragona, mountain olm oak forests in the east of the region, or beech forests of great economical/cultural relevance across the studied area.

Management of the insect pest *C. perspectalis* must be carefully treated. Despite the use of bacterial pesticide *Bacillus thuringensis* was proved to be lethal for the box tree moth (Matošević 2013; Wan et al. 2014), the application of pesticides is very expensive and its effectivity at the landscape scale is not demonstrated yet because it may interfere with the density-dependent mortality dynamics (Liebhold 2012). Also, the use of pesticides is under discussion because it is difficult to ensure that treatments actually affect the targeted species only (Isenring, 2010; Pimentel, 1995). Similar controversy has arisen when considering the introduction of natural *C. perspectalis* enemies from the native area, like *Chelonus tabonus* Sonan. as proposed by Wan et al., (2014). Although this Hymenoptera belongs to a subfamily known to usually be host specific, further research should be realized before implementing such a measure in new habitats (Liebhold 2012; Wan et al. 2014). Less intrusive management strategies include the removal of dead boxwoods and mechanical removal of larvae (Kenis et al., 2013), but this strategy is not feasible at broad landscape scale, only in particular gardens or specific endangered highly-valuable forest stands. Ayres and Lombardero (2018) proposed adaptative science and management as the most adequate strategy. Such means management measures based on empirically demonstrated theories, taking advantage of shared knowledge among regions (in this case, native and invaded areas), and pushing agreements between managers, scientists, and decision-makers. In this paper we also pledge for adaptative management and we provide important insights based on native and invaded areas (see SDMCyd construction in Canelles et al., 2021b) to design adequate management strategies. We anticipate that *C. perspectalis* distribution and impact will not exponentially increase, but it will be cyclical. Further, climate change is projected to mitigate pest impact in some regions, as happens with other forests pests (Ims et al. 2008; Johnson et al. 2010). We should also consider that *C. perspectalis* is an invasive species recently arrived in the study area, so natural enemies such as birds, bats or other insectivores may become pest controllers in the future (Bakay and Kollár 2018).

Interactions between boxwood disturbances should be also considered by forest managers. Despite we did not find that the interaction between *C. perspectalis* occurrence and drought was relevant for the boxwood viability, other interactions may be significant (for instance, between fire and insect pest as mentioned above). In this interaction dynamics two elements must be remarked: First, management is crucial in facilitating/hindering such interactions like the failure to control wildfires may predispose forests to outbreaks (Billings et al. 2014), or fire suppression may result in changes in forest composition increasing susceptibility to forest insect outbreaks (McCullough et al. 1998). Second, simulation models and spatially explicit simulations are essential tools in disturbance interactions management as they can operate at broad spatio-temporal scales and can be used to project possible future scenarios (Canelles et al. 2021a).

Finally, we emphasize that improved monitoring and control of the *C. perspectalis* pest, wildfires, and drought in the following years (as done in Catalonia since 2019) combined with qualitative science studies are crucial for the conservation of boxwoods in the Southern Pyrenees.

Conclusions

B. sempervirens in Southern Pyrenees is facing several disturbances that will lead to a decay of the population. *C. perspectalis* is now an important driver of such decay, but its exponential growth registered since its arrival in the area is projected to flow onto a cyclic dynamic. Also, climate change is predicted to reduce the suitability area of the insect and the severity of the impacts. Conversely, climate change will lead to an increase in burned area, and thus boxwood mortality by fire, as well as by drought.

Boxwood decay is not even distributed across the territory. *C. perspectalis* impact will be concentrated in Girona and Barcelona provinces and its climate suitability is limited at higher elevations. Fire and drought are also driven by an elevation pattern, affecting more low land populations. Such disturbance distribution imply that some boxwood habitats are more endangered (like forests with understory of boxwood) than others (like open shrub forest). We encourage forest managers to apply adaptive strategies according to these disturbances trends and prioritize endangered areas, as well as we emphasize the need of monitoring future boxwood populations and their associated disturbances.

References

Allstadt AJ, Haynes KJ, Liebhold AM, Johnson DM (2013) Long-term shifts in the cyclicity of outbreaks of a forest-defoliating insect. *Oecologia* 172:141–151. https://doi.org/10.1007/s00442-012-2474-x

Amatulli G, Camia A, San-Miguel-Ayanz J (2013) Estimating future burned areas under changing climate in the EU-Mediterranean countries. *Sci Total Environ* 450–451:209–222. https://doi.org/10.1016/j.scitotenv.2013.02.014

Artola J (2019) Seguiment de la biologia i la fenologia de la papallona del boix (*Cydalima perspectalis*) al Parc Natural de la Sona Volcànica de la Garrotxa. General Cataluna; Dep Territ i Sostenibilitat

Ayres MP, Lombardero M (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci Total Environ* 62:. https://doi.org/10.1016/S0048-9697(00)00528-3

Ayres MP, Lombardero MJ (2018) Forest pests and their management in the Anthropocene. *Can J For Res* 48:292–301. https://doi.org/10.1139/cjfr-2017-0033

Bakay L, Kollár J (2018) The spread rate of *Cydalima perspectalis* (Walker 1859) in Slovakia (2013-2015). *Plants Urban Areas Landsc* 51–54. https://doi.org/https://doi.org/10.15414/PUAL/2018.51-54

Bassols E, Oliveras J (2014) *Cydalima perspectalis* (Walker , 1859), una nova espècie invasora a Catalunya (Lepidoptera). *Butll Soc Cat Lep* 105:71–78

Bates OK, Ollier S, Bertelsmeier C (2020) Smaller climatic niche shifts in invasive than non-invasive alien ant species. *Nat Commun* 11:1–8. https://doi.org/10.1038/s41467-020-19031-1

Batllori E, Parisien MA, Krawchuk MA, Moritz MA (2013) Climate change-induced shifts in fire for Mediterranean ecosystems. *Glob Ecol Biogeogr* 22:1118–1129. https://doi.org/10.1111/geb.12065

Bebber DP, Ramotowski MAT, Gurr SJ (2013) Crop pests and pathogens move polewards in a warming world. *Nat Clim Chang* 1–4. https://doi.org/10.1038/NCLIMATE1990

Billings RF, Clarke SR, Mendoza VE, et al (2014) Bark beetle outbreaks and fire: A devastating combination for central America’s pine forests. *For Chem Rev* 124:10–15

Blackburn TM, Pyšek P, Bacher S, et al (2011) A proposed unified framework for biological invasions. *Trends Ecol Evol* 26:333–339. https://doi.org/10.1016/j.tree.2011.03.023

Bouchard M, Aquilué N, Périé C, Lambert MC (2019) Tree species persistence under warming conditions: A key driver of forest response to climate change. *For Ecol Manage* 442:96–104. https://doi.org/10.1016/j.foreco.2019.03.040

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. *Ecol Modell* 157:281–300. https://doi.org/https://doi.org/10.1016/S0304-3800(02)00200-4Get

Bradshaw CJA, Leroy B, Bellard C, et al (2016) Massive yet grossly underestimated global costs of invasive insects. *Nat Commun* 7:. https://doi.org/10.1038/ncomms12986

Bras A, Avtzis DN, Kenis M, et al (2019) A complex invasion story underlies the fast spread of the invasive box tree moth (*Cydalima perspectalis*) across Europe. *J Pest Sci* (2004) 92:1187–1202. https://doi.org/10.1007/s10340-019-01111-x

Broncano MJ, Retana J (2004) Topography and forest composition affecting the variability in fire severity and post-fire regeneration occurring after a large fire in the Mediterranean basin. *Int J Wildl Fire* 13:209–216. https://doi.org/10.1071/WF03036

Brotons L, Aquilué N, de Cáceres M, et al (2013) How fire history, fire suppression practices and climate change affect wildfire regimes in Mediterranean landscapes. *PLoS One* 8:. https://doi.org/10.1371/journal.pone.0062392

Burriel JA (2017) Els mapes de perill d’incendi forestal. In: II jornades: Incendis forestals i recerca. Girona

Camarero JJ, Bigler C, Linares JC, Gil-Pelegrín E (2011) Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. *For Ecol Manage*. https://doi.org/10.1016/j.foreco.2011.05.009

Canelles Q, Aquilué N, James PMA, et al (2021a) Global review on interactions between insect pests and other forest disturbances. *Landsc Ecol* 7:. https://doi.org/10.1007/s10980-021-01209-7

Canelles Q, Bassols E, Vayreda J, Brotons L (2021b) Predicting the potential distribution and forest impact of the invasive species *Cydalima perspectal*is in Europe. *Ecol Evol* 1–15. https://doi.org/10.1002/ece3.7476

Carreras J (2004) La cartografia dels hàbitats de Catalunya: una eina per conèixer i gestionar el territori. *Omnis Cell* 7:52–56

Carreras J, Ferré A, Oliva F, Pérez-Prieto D (2014) Avaluació dels canvis dels canvis en els hàbitats en els hàbitats a a Catalunya Catalunya. Generalitat de Catalunya, Barcelona

Casals P, Rios AI (2018) Burning intensity and low light availability reduce resprouting ability and vigor of *Buxus sempervirens* L. after clearing. *Sci Total Environ* 627:403–416. https://doi.org/10.1016/j.scitotenv.2018.01.227

Comas L, Gracia M, Vayreda J (2013) Inventari de boscos singulars de Catalunya. *L'Atzavara* 0:29–36

Cooke BJ, Lorenzetti F (2006) The dynamics of forest tent caterpillar outbreaks in Québec, Canada. *For Ecol Manage* 226:110–121. https://doi.org/10.1016/j.foreco.2006.01.034

Dale VH, Joyce LA, McNulty S, et al (2001) Climate change and forest disturbances. *Bioscience* 51:723. https://doi.org/10.1641/0006-3568(2001)051[0723:ccafd]2.0.co;2

De Jong SM, Addink EA, Hoogenboom P, Nijland W (2012) The spectral response of *Buxus sempervirens* to different types of environmental stress - A laboratory experiment. *ISPRS J Photogramm Remote Sens* 74:56–65. https://doi.org/10.1016/j.isprsjprs.2012.08.005

Decocq G, Bordier D, Wattez J-R, Racinet P (2004) A practical approach to assess the native status of a rare plant species: the controverse of *Buxus sempervirens* L. in northern France revisited. *Plant Ecol* 173:139–151. https://doi.org/10.1023/B

Di Domenico F, Lucchese F, Magri D (2012) *Buxus* in Europe: Late Quaternary dynamics and modern vulnerability. *Perspect Plant Ecol Evol Syst* 14:354–362. https://doi.org/10.1016/j.ppees.2012.07.001

Duane A, Aquilué N, Canelles Q, et al (2019a) Adapting prescribed burns to future climate change in Mediterranean landscapes. *Sci Total Environ* 677:68–83. https://doi.org/10.1016/j.scitotenv.2019.04.348

Duane A, Kelly L, Giljohann K, et al (2019b) Disentangling the influence of past fires on subsequent fires in Mediterranean landscapes. *Ecosystems* 22:1338–1351. https://doi.org/10.1007/s10021-019-00340-6

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *TREE* 14:135–139. https://doi.org/https://doi.org/10.1016/S0169-5347(98)01554-7

Fares S, Mugnozza S, Corona P, Palahí M (2015) Five steps for managing Europe's forests: Support resilience and promote carbon storage, say Silvano Fares and colleagues. *Nature* 519:407–409. https://doi.org/10.1038/519407a

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315. https://doi.org/10.1002/joc.5086

Gazol A, Sangüesa-barreda G, Camarero JJ, Miranda JC (2020) Forecasting forest vulnerability to drought in Pyrenean silver fir forests showing dieback. *Frontiers in Forests and Global Change*, *3*, 36. https://doi.org/10.3389/ffgc.2020.00036

Guisan A, Thuiller W, Zimmermann NE (2017) Habitat Suitability and Distribution Models sith applications in R. cambridge University Press

Gustafson EJ, Shvidenko AZ, Sturtevant BR, Scheller RM (2010) Predicting global change effects on forest biomass and composition in south-central Siberia. *Ecol Appl* 20:700–715. https://doi.org/https://doi.org/10.1890/08-1693.1

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a Receiver Operating Characteristic (ROC) curve. *J Med Internet Res* 143:29–36. https://doi.org/10.1148/radiology.143.1.7063747

Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. *Conserv Biol* 22:534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Hormaetxe K, Becerril JM, Hernández A, et al (2007) Plasticity of photoprotective mechanisms of *Buxus sempervirens* L. leaves in response to extreme temperatures. *Plant Biol* 9:59–68. https://doi.org/10.1055/s-2006-924456

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *J Appl Ecol* 46:10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Ibàñez JJ, Burriel JA, Pons X (2002) El Mapa de Cobertes del Sòl de Catalunya: Una eina per al coneixement, la planificació i la gestió del territori. *Perspect Territ* 10–25

Ims RA, Henden JA, Killengreen ST (2008) Collapsing population cycles. *Trends Ecol Evol* 23:79–86. https://doi.org/10.1016/j.tree.2007.10.010

Johnson DM, Büntgen U, Frank DC, et al (2010) Climatic warming disrupts recurrent Alpine insect outbreaks. *Proc Natl Acad Sci U S A* 107:20576–20581. https://doi.org/10.1073/pnas.1010270107

Karger DN, Conrad O, Böhner J, et al (2017) Climatologies at high resolution for the earth's land surface areas. *Sci Data* 4:1–20. https://doi.org/10.1038/sdata.2017.122

Keane RE, Cary GJ, Davies ID, et al (2004) A classification of landscape fire succession models: Spatial simulations of fire and vegetation dynamics. *Ecol Modell* 179:3–27. https://doi.org/10.1016/j.ecolmodel.2004.03.015

Keane RE, McKenzie D, Falk DA, et al (2015) Representing climate, disturbance, and vegetation interactions in landscape models. *Ecol Modell* 309–310:33–47. https://doi.org/10.1016/j.ecolmodel.2015.04.009

Kelsey RG, Joseph G (2003) Ethanol in ponderosa pine as an indicator of physiological injury from fire and its relationship to secondary beetles. *Can J For Res* 33:870–884. https://doi.org/10.1139/x03-007

Kingsolver JG, Arthur Woods H, Buckley LB, et al (2011) Complex life cycles and the responses of insects to climate change. *Integr Comp Biol* 51:719–732. https://doi.org/10.1093/icb/icr015

Leuthardt FLG (2013) Distribution , life history , food choice and chemical ecology of the invasive box-tree pyralid *Cydalima perspectalis*. University of Basel

Liebhold AM (2012) Forest pest management in a changing world. *Int J Pest Manag* 58:289–295. https://doi.org/10.1080/09670874.2012.750910

Lombardero MJ, Ayres MP (2011) Factors influencing bark beetle outbreaks after forest fires on the Iberian Peninsula. *Environ Entomol* 40:1007–1018. https://doi.org/10.1603/en11022

Marquaridt DW (1970) Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics* 12:591–612. https://doi.org/10.1080/00401706.1970.10488699

Maruyama T, Shinkaji N (1987) Studies on the life cycle of the box-tree pyralid, *Glyphodes perspectalis* (Walker) (Lepidoptera: Pyralidae). I. Seasonal adult emergence and developmental velocity. *Jpn J Appl Entomol Zool* 31:226–232

Matošević D (2013) Box Tree Moth (*Cydalima perspectalis* , Lepidoptera ; Crambidae), New Invasive Insect Pest in Croatia. *South-East Eur* 4:89–94

McCullough DG, Werner RA, Neumann D (1998) Fire and insects in northern and boreal forest ecosystems of North America. *Annu Rev Entomol* 43:107–127. https://doi.org/10.1146/annurev.ento.43.1.107

Meigs GW, Zald HSJ, Campbell JL, et al (2016) Do insect outbreaks reduce the severity of subsequent forest fires? *Environ Res Lett* 11:. https://doi.org/10.1088/1748-9326/11/4/045008

Mitchell R, Chitanava S, Dbar R, Kramarets V (2018) Identifying the ecological and societal consequences of a decline in *Buxus* forests in Europe and the Caucasus. *Biol Invasions.* https://doi.org/10.1007/s10530-018-1799-8

Monfort-Bague IP, Vega-García C, Jürguens J, et al (2020) Stem selection reduces the resprouting vigor of box-tree (*Buxus sempervirens* L.) understory in sub-Mediterranean pine forest. *Eur J For Res*. https://doi.org/10.1007/s10342-020-01297-1

Myers JH (1988) Can a general hypothesis explain population cycles of forest lepidoptera? *Adv Ecol Res* 18:179–242. https://doi.org/10.1016/S0065-2504(08)60181-6

Myers JH, Cory JS (2013) Population cycles in forest lepidoptera revisited. *Annu Rev Ecol Evol Syst* 44:565–592. https://doi.org/10.1146/annurev-ecolsys-110512-135858

Nacambo S, Leuthardt FLG, Wan H, et al (2014) Development characteristics of the box-tree moth *Cydalima perspectalis* and its potential distribution in Europe. *J Appl Entomol* 138:14–26. https://doi.org/10.1111/jen.12078

Niinemets Ü, Valladares F (2006) Tolerence to shade, drought, and waterlogging of temperate northern hemisphere trees and shrub. *Ecol Monogr* 76:521–547

Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol Modell* 213:63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Petrie MD, Wildeman AM, Bradford JB, et al (2016) A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. For *Ecol Manage* 361:328–338. https://doi.org/10.1016/j.foreco.2015.11.028

Petrie R, Denvil S, Ames S, et al (2021) Coordinating an operational data distribution network for CMIP6 data. *Geosci Model Dev* 14:629–644. https://doi.org/10.5194/gmd-14-629-2021

Pimentel D (1995) Amounts of pesticides reaching target pests: Environmental impacts and ethics. *J Agric Environ Ethics* 8:17–29. https://doi.org/10.1007/BF02286399

Poitou L, Bras A, Pineau P, et al (2020) Diapause regulation in newly invaded environments : termination timing allows matching novel climatic constraints in the box tree moth, *Cydalima perspectalis* (Lepidoptera: Crambidae). *Insects* 11:. https://doi.org/https://doi.org/10.3390/insects11090629

Robert LE, Sturtevant BR, Kneeshaw D, et al (2020) Forest landscape structure influences the cyclic-eruptive spatial dynamics of forest tent caterpillar outbreaks. *Ecosphere* 11:. https://doi.org/10.1002/ecs2.3096

Robinet C, Baier P, Pennerstorfer J, et al (2007) Modelling the effects of climate change on the potential feeding activity of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Notodontidae) in France. *Glob Ecol Biogeogr* 16:460–471. https://doi.org/10.1111/j.1466-8238.2006.00302.x

Robinet C, Roques A (2010) Direct impacts of recent climate warming on insect populations. *Integr Zool* 5:132–142. https://doi.org/10.1111/j.1749-4877.2010.00196.x

Rosenberger DW, Venette RC, Aukema BH (2017) Development of an aggressive bark beetle on novel hosts: Implications for outbreaks in an invaded range. *J Appl Ecol* 55:1526–1537. https://doi.org/10.1111/1365-2664.13064

Sakai AK, Allendorf FW, Holt JS, et al (2001) The population biology of invasive species. *Annual review of ecology and systematics*, *32*(1), 305-332.

Sangüesa-Barreda G, Linares JC, Camarero JJ (2015) Reduced growth sensitivity to climate in bark-beetle infested Aleppo pines: Connecting climatic and biotic drivers of forest dieback. *For Ecol Manage* 357:126–137. https://doi.org/10.1016/j.foreco.2015.08.017

Seidl R, Thom D, Kautz M, et al (2017) Forest disturbances under climate change. *Nat Clim Chang* 7:395–402. https://doi.org/10.1038/nclimate3303

Silva JS, Vaz P, Moreira F, et al (2011) Wildfires as a major driver of landscape dynamics in three fire-prone areas of Portugal. *Landsc Urban Plan* 101:349–358. https://doi.org/10.1016/j.landurbplan.2011.03.001

Suárez-Muñoz M, Bonet-García F, Hódar JA, et al (2019) INSTAR: An Agent-Based Model that integrates existing knowledge to simulate the population dynamics of a forest pest. *Ecol Modell* 411:108764. https://doi.org/10.1016/j.ecolmodel.2019.108764

Tenow O, Nilssen AC, Bylund H, et al (2013) Geometrid outbreak waves travel across Europe. *J Anim Ecol* 82:84–95. https://doi.org/10.1111/j.1365-2656.2012.02023.x

Trabaud L (1994) Postfire plant community dynamics in the Mediterranean Basin. In: The role of fire in Mediterranean-type ecosystems. *Springer*, pp 1–15

Turco M, Rosa-Cánovas JJ, Bedia J, et al (2018) Exacerbated fires in Mediterranean Europe due to anthropogenic warming projected with non-stationary climate-fire models. *Nat Commun* 9:1–9. https://doi.org/10.1038/s41467-018-06358-z

Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849. https://doi.org/10.1358/dot.2011.47.2.1576694

Vandermeer J (2006) Oscillating populations and biodiversity maintenance. *Bioscience* 56:967–975. https://doi.org/10.1641/0006-3568(2006)56[967:OPABM]2.0.CO;2

Vermeij GJ (1996) An agenda for invasion biology. *Biol Conserv* 78:3–9. https://doi.org/10.1016/0006-3207(96)00013-4

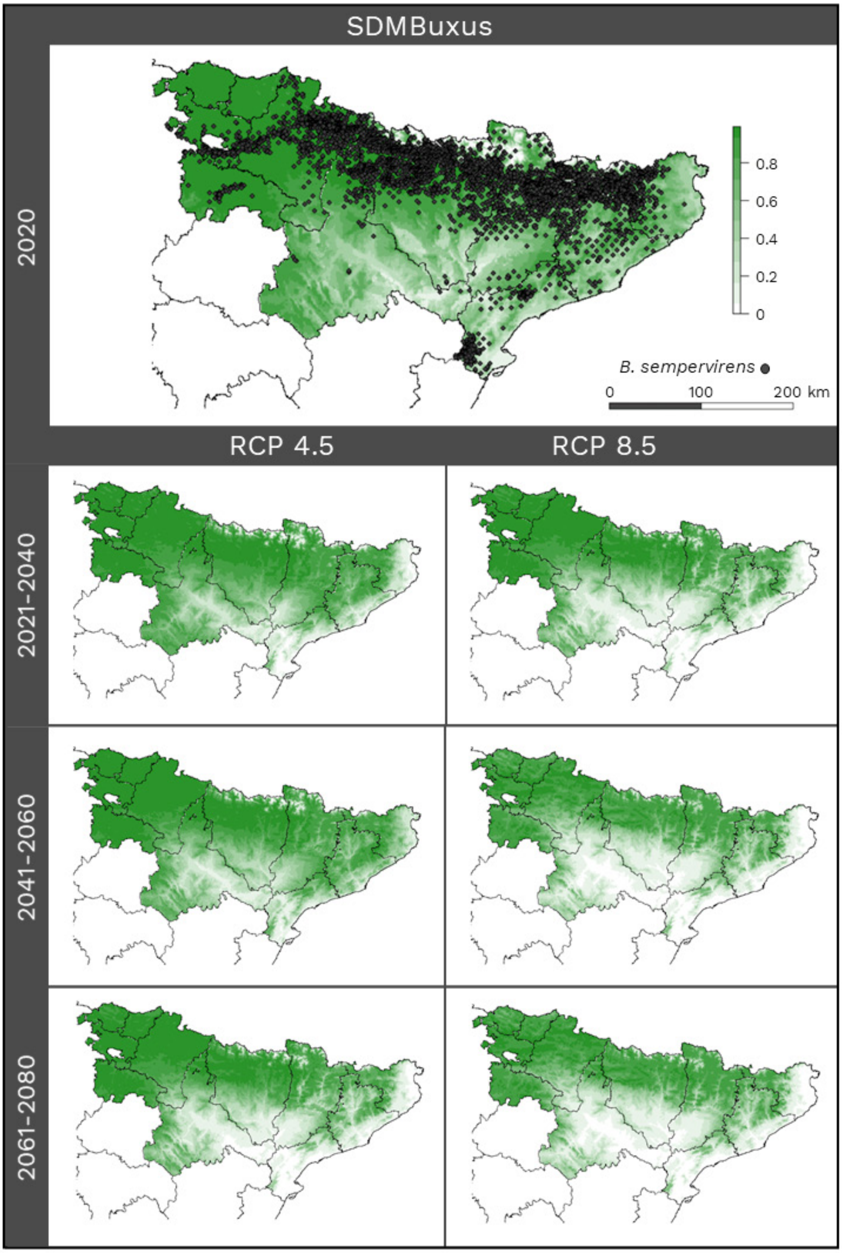
Villanueva JA (2005) Tercer inventario forestal nacional (1997–2007). Minist Medio Ambient ICONA

Wan H, Haye T, Kenis M, et al (2014) Biology and natural enemies of *Cydalima perspectalis* in Asia: Is there biological control potential in Europe? *J Appl Entomol* 138:715–722. https://doi.org/10.1111/jen.12132

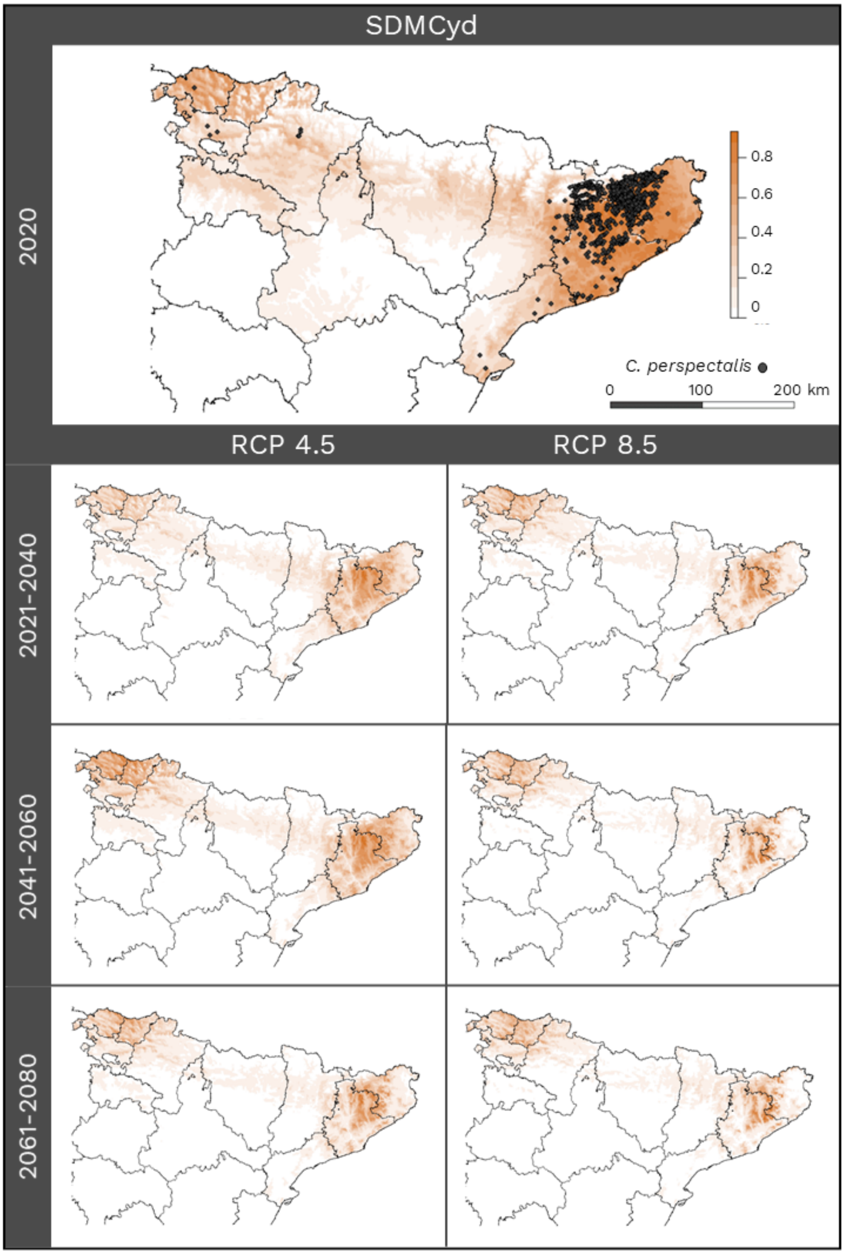
Williams AP, Allen CD, Macalady AK, et al (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat Clim Chang* 3:292–297. https://doi.org/10.1038/nclimate1693

Wilson WG, Lundberg P, Vázquez DP, et al (2003) Biodiversity and species interactions: Extending Lotka-Volterra community theory. *Ecol Lett* 6:944–952. https://doi.org/10.1046/j.1461-0248.2003.00521.x

Wong CM, Daniels LD (2017) Novel forest decline triggered by multiple interactions among climate, an introduced pathogen and bark beetles. *Glob Chang Biol* 23:1926–1941. https://doi.org/10.1111/gcb.13554



▶ SUPPLEMENTARY FIGURE 1
Species Distribution Model for *B. sempervirens* in the study area. Future projections under climate scenarios RCP 4.5 and RCP 8.5 are presented. Species presences in 2020 are added as black points according to the locations reported in GBIF.



▶ **SUPPLEMENTARY FIGURE 2**
Species Distribution Model for *C. perspectalis* in the study area. Future projections under climate scenarios RCP 4.5 and RCP 8.5 are presented. Species presences are added as black points according to the locations reported in GBIF, Alerta Forestal and the Agents Rurals de la Generalitat de Catalunya.

General discussion and conclusions

Forest insect pests are changing in an anthropized world. Although insects are part of the forest landscape dynamics, an increase in their frequency and severity has been experienced in the recent decades. Forest insects often exceed the ecosystem threshold of tolerance and may cause severe damages to the ecosystem. The factors behind these dynamics are complex and directly or indirectly conditioned by human activity. In this thesis I analyzed the role of insect pests as a forest landscape driver and I deepened into the study of invasive species (Chapter 2 and 3), the effects of climate change (Chapter 3), and insect pest interactions between other disturbances (Chapter 1 and 3) as main factors defining insect pest impacts on ecosystems. Specifically, I used the case of the box tree moth (*Cydalima perspectalis*) as a prime example of invasive insect pest impacting the forest landscape.

Studying invasive insects

Invasive species are increasing in recent decades mainly due to international trades (Hulme 2009; Bradshaw et al. 2016). However, many of the alien species that arrive to new areas fail in their invasion process, whether in the transport, the introduction, the establishment, or the spread stage (Blackburn et al. 2011). Species reaching the spread stage are considered invasive but may have either no impact on the invaded area, a discernible impact but without effects at the population or community level, a reversible impact for the invaded community or a fatally irreversible impact (Blackburn et al. 2014). Therefore, here I emphasized the importance of differentiating the presence of the invasive species from its impact.

Modeling dispersion and impact separately facilitates the understanding of the factors behind each process, and adapting management strategies. Guisan et al. (2017) described that the presence of a species is the result of a combination between its dispersal capacity, the biotic environment, and the abiotic environment. I used this theoretical framework to describe not only the presence of the species, but also the ecological niche for severe impact (TABLE 1). For example, in the study case presented here, the presence of the invasive insect *C. perspectalis* depended on the distribution of its host plant as the main biotic factor and on the insect dispersal capacity, in turn conditioned on its flight ability and involuntary introductions by humans and other animals. Although the abiotic factors (in our case climate variables) were not relevant to define the presence of the species, they were essential to define the severity of its impact.

The stage of invasion of the box tree moth (*C. perspectalis*) has already passed the arrival and establishment phases in Southern Pyrenees (where it is present since 2014; Bassols and Oliveras 2014) and it is in the process of spreading throughout the territory. The severe impact on the boxwoods was first identified in 2017 in the region of Girona and followed an East-West spread since then. The modeling of its impact demonstrated that *C. perspectalis* is a habitat generalist species (it has no requirements related to the fragmentation or heterogeneity of the habitat) and proved that severe defoliation impact was restricted by climate suitability. By adjusting a species distribution model (SDM), I concluded that mild climate conditions with low precipitation seasonality combined with small temperature diurnal range defined the suitability for a severe impact of *C. perspectalis*. These climatic variables were described to influence insect development in general (Herms 2004; Suppo et al. 2020) and the case of *C. perspectalis* in particular (Nacambo et al. 2014). Climate suitability for *C. perspectalis* defined a certain continentality effect: climate conditions in the coast are more suitable than in inland areas or higher elevations.

An important finding thus is that, although *C. perspectalis* can be found inland and at high elevation locations, severe impacts caused by the species are restricted to areas where climate suitability is higher. Severe impact can lead to total boxwood defoliation and, despite the resprouting capability of the hosting plant, it might lead to a lack of food for the insect in the following seasons. Consequently, a cyclical relationship is established as an extension of the Lotka-Volterra model that tightly links consumer (i.e., *C. perspectalis*) and resources (i.e., boxwood) dynamics as happens with other insect pests (Wilson et al. 2003; Cooke and Lorenzetti 2006; Vandermeer 2006; Allstadt et al. 2013; Tenow et al. 2013). In the case of box tree moth, the periodicity and severity of this cyclic pattern is conditioned by the capacity and timing of boxwood regeneration, two parameters that are still not well defined due to the recent arrival of *C. perspectalis*. At the same time, *C. perspectalis* is not in equilibrium with the invaded habitat, so other factors can influence its impact (e.g., fertility patterns linked to population density, parasitism, or predation relationships) until the species will be naturalized in the ecosystem (Myers and Cory 2013).

The role of climate change

Climate change is described as a key driver of change defining the impact of forest pests and invasive species (Jactel et al. 2019). Insects are responsive to climate change due to their sensitivity to temperature, short generation times and high flight capacity. Hence, climate change influences the expansion of species (new climatic conditions push insects to new localities, usually because of the increasing temperatures at higher latitudes and elevations), insect abundance (in temperate climates, insects respond positively to temperature via more generations per year or less winter mortality during the diapause), the response capability of host plants and, consequently, the intensity of insect pest outbreaks (Pureswaran et al. 2018; Jactel et al. 2019). However, the effects of climate change on forest insects cannot be generalized to all species even within the same guild or biome. For example, both positive and negative effects of climate change can occur simultaneously, as observed in the pine processionary moth (*Thaumetopoea pityocampa*) during summer heat waves in 2003 (Pureswaran et al. 2018). Such waves led to a collapse of the front edge population in France by killing early stages of the insect, while triggering a record annual expansion in the Italian Alps by facilitating female flight (Battisti et al. 2006; Robinet et al. 2014). In the case of invasive species, traits such as short generation times, rapid dispersal, or environmental plasticity could be advantageous in a changing climate, while native species more established in the ecosystem are not as moldable as the previous ones (Dukes and Mooney 1999; Hellmann et al. 2008).

Although climate change influences the fitness and expansion of insects, insect impacts on forests are also conditioned by the response of the host plant (TABLE 1). Thus, the effects of climate change on the host plant also determine the dynamics of forest pests. In Chapter 1 of this thesis, I described that drought-stressed trees synthesize chemicals that act as insect attractants and, at the same time, may reduce their leaf and stem-water potential limiting their resistance to insect attacks (Kelsey et al. 2014; Anderegg et al. 2015; Klutsch et al. 2017). In addition, when insects attack the crown and roots of a tree, they compromise water-regulation capacity and, therefore, trees become more susceptible to later episodes of extreme drought leading to higher mortality rates (Allen et al. 2010; Altmann 2013). These are only few cases of indirect effects of climate change on forest insects and their impacts as more examples include interactions with other forest disturbances that are also sensitive to climate, such as storms, floods, windstorms, or the wildfire regime (discussed below).

In the case of *C. perspectalis*, the projections of its climate suitability under climate change conditions described a reduction in its suitable area and a reduction of its impact (studied in Chapter 3). The predicted increase in temperatures and concentration of precipitation in shorter periods are detrimental to the development of *C. perspectalis*, which develops under more stable climatic conditions. I also modeled the climate suitability of *Buxus sempervirens* to understand the response capacity of the host plant under climate change conditions. I confirmed that *B. sempervirens* is a drought tolerant species (Niinemets and Valladares 2006) and that its response to *C. perspectalis* attacks is not expected to be strongly conditioned by climate change. Thus, I concluded that *C. perspectalis* is an example of invasive species not favored by climate change as I predict a reduction of its suitable area and that the drought experienced by its host plant will not accentuate the insect impact.

Forest disturbances interacting with insect pests

The effects of insect pests on forest landscape are not limited to direct herbivory and xylofagy, but also involve different indirect impacts when interacting with other disturbances. Disturbances disrupt the structure and composition of ecosystems and change the physical environment causing temporary disorganization of the ecosystem and, consequently, altering the susceptibility of forests to new disturbances (Turner 2010). In Chapter 3 of this thesis, I described the main interactions impacting landscape dynamics and I analyzed the mechanisms behind them. Most of the revised papers were focused on forests pests interacting with fire while interactions with drought, pollution, storms, wind, forest diseases, or other pests received much less attention. These interactions may be synergistic, antagonistic, or even non-existent in some cases. Although interactions were described in different insect feeding guild, spatial and temporal scales, I found that any of these aspects were directly linked to interaction likelihood, avoiding generalist conclusions. I strongly recommend differentiating when a disturbance increases the occurrence likelihood of another with respect to when a disturbance increases the severity of the subsequent one is adequate for a better understanding and management of disturbance interactions (TABLE 1; (James et al. 2011; Meigs et al. 2016).

FIELD	MAIN CHALLENGES
Insect pest outbreaks	Describing the future potential impact of the insect pest.
	Prioritizing the management of those areas and habitats more vulnerable according to their ecological and cultural value.
Invasive species	Integrating information from both native and invaded area since the invasive species is not in equilibrium with the invaded ecosystem.
	Identifying the invasion stage and making distinction between the presence and the impact of the invasive species.
	Describing the main species requirements and restrictors.
Climate change	Analyzing the climate change impact to the insect species but also to the host plant species.
Disturbance interactions	Evaluating not only the likelihood of an interaction, but also other features such as insect spread or disturbance severity.
	Identifying the emergence of novel interactions as a consequence of current dynamics.
	Considering interactions at different spatial and temporal scales.

▶ TABLE 1
Summary of the main challenges in the study and management in different fields of forest insect pests.

Studying the interaction between insect pests and other disturbances offers a comprehensive description of the impacts on the forest landscape. At the same time, it allows anticipation of new interactions that will result from continued global change (TABLE 1). The increase of invasive species may lead to new insect pest regimes as well as new interactions, as I studied in this thesis. Land use changes may also influence fitness of insect pests or shift their range of expansion. Thus, researchers and managers should acknowledge that current dynamics and management policy effects extend beyond the short-term and local scale, and they should pay special attention not only to current forest pests but also to those that may have future impacts.

I studied the potential interaction between *C. perspectalis* attacks and drought through climatic requirements for the boxwood regeneration after severe defoliation. However, such interaction did not significantly alter the population dynamics of boxwood neither *C. perspectalis*. Still, I proposed the analysis of other interactions, such as the lack of boxwood in some understory forests because of *C. perspectalis* induced defoliation may influence the fuel availability for subsequent fires, as future study challenges.

Challenges in the study and management of insect pests

During the development of this thesis, I identified and discussed different challenges for the study of forest pest and invasive species impacts. Species distribution models (SDMs) are commonly used to predict the potential distribution range of invasive species (Uden et al. 2015). SDMs are built on the general concept of fundamental niche and are based on the species occurrence and associated environmental data. I used the SDM methodology not only to predict the species distribution, but also the potential severe impact occurrence. As exposed above, differentiation of distribution and impact allow to distinguish the main factors and mechanisms behind each process and a better understand of the species dynamics. The application of species distribution models in the case of invasive species (SDMi) is under discussion because it may contradict two SDM assumptions: (a) ecological niches are stable in space and time, and (b) the studied species is in quasi-equilibrium with the environment (Elith and Graham 2009; Gallien et al. 2010; Barbet-Massin et al. 2018). Thus, for an adequate understanding of the species, it is necessary to combine information from the original area and the invaded area to develop a synoptic view of the mechanisms involved in the invasion process (Pyšek et al. 2010). I used information from the native area of the species to calibrate the data of the invaded area (Gallien et al. 2012), obtaining satisfactory results of the species ecological niche.

Furthermore, I have emphasized the adequacy of spatially explicit simulation models in order to understand and predict the future of insect pest dynamics. To do so, I analyzed the methodology developed by different researchers (Chapter 1) and finally I designed, built, and applied my own model for the study case of the box tree moth. I emphasize the use of such models for two main reasons: First, simulation models are able to explore dynamics to distant futures, that is crucial in the case of insect pest disturbances because of the long-term spatial legacies they may create and the host-insect cyclic dynamics they may induce, as seen in the case of *C. perspectalis* (Robert et al. 2020). Second, such modelling frameworks allow testing the relevance of certain processes and weighting key parameters that are difficult to empirically estimate, but that may have a significant incidence in landscape dynamics as is the case of the timing in disturbance processes or interactions between disturbances that I analyzed in Chapter 3 (Bouchard et al. 2019).

In this thesis I do not explicitly analyze forest pest management strategies, but I do emphasize that it is an essential unresolved issue that requires greater coordination between researchers that study species biology and impacts, managers who design and apply control measures, and forest owners who have economic interests. Therefore, I emphasize that the type of study presented here offers an opportunity to deepen on the knowledge of forest pests and invasive species while establishing an essential basis on which to build management strategies.

Conclusions

1. Forest insect pests are integrated elements of forest landscape dynamics, but they are shifting in a global change context pushed by anthropic pressures. Main drivers of insect pest dynamics are land use changes, climate change, and arrival of new invasive species due to international trade.

2. The invasive species *Cydalima perspectalis* depends on the presence of its host plant, its availability to spread and its climate suitability. Habitat composition variables such as forest cover, habitat fragmentation and heterogeneity resulted non-significant to describe *C. perspectalis* distribution and impact.

3. Climate suitability for *C. perspectalis* is characterized by limited seasonality of precipitation and temperatures and low diurnal ranges These conditions are common in Western Europe and in coastal areas. In Southern Pyrenees, such climate suitability is usually found at low elevation and more frequently in some boxwood habitats, like forests with understory of boxwood, than others like open shrub formations.

4. Climate suitability is a more restrictive variable to *C. perspectalis* severe impact than to the species distribution, indicating that *C. perspectalis* may be present in some areas where its impact may be limited.

5. Climate change is one of the main drivers of insect pests and their consequent impacts on forest landscape dynamics. It can promote or limit the establishment of invasive insect species, shift the geographic distribution, increase the number of insect generations per year, regulate predators or competitive species, determine the response capability and viability of the host plants, and lead to more extreme disturbance interactions. In the case of *C. perspectalis*, climate change is projected to reduce the species suitable area and, therefore, the severity of defoliation. Thus, I concluded that *C. perspectalis* is an example of invasive species not favored by climate change.

6. Defoliation of *Buxus sempervirens* by *C. perspectalis* may lead to a cyclic dynamic between the host plant and the insect as an extension of the Lotka-Volterra model that links consumer and resources.

7. Other disturbances may challenge *B. sempervirens* viability, mainly wildfire and severe drought. These disturbances impacts are increased under climate change conditions.

8. Interactions between insect pests and other disturbances are critical drivers of forest dynamics worldwide. Connections between disturbances are complex including different spatial and temporal scales (from physiology to landscape and from days to century, respectively) and various types of interaction (influences on the likelihood, severity, spread or insect fitness). Any of such disturbance features is significantly linked to the occurrence of disturbance interaction.

9. Fire interacting insect pests are broadly studied, although interaction with drought, pollution, other diseases, storms, landslides, and management have also been considered.

10. Forest disturbances and their interactions with insect pests are predicted to increase due to global change as insect pests are strongly influenced by climate. Also, novel interactions may emerge as a result of increasing pollution, land use changes and arrival of new invasive species.

11.

Differentiation of disturbance likelihood versus disturbance severity is recommended for the study of disturbance interactions.

12. Differentiation of the presence of the species (resulting from its spread) versus the severe defoliation caused (resulting from its impact) is appropriate when analyzing insect pest outbreaks and, specially, in the case of invasive species.

13. The combination of SDMs and simulation models are presented as recommendable tools to study the current and potential impact of insect pests and their interactions with other disturbances. SDMs allow to anticipate invasive species spread and impact even though the species is not in equilibrium with the invaded environment.

14. Spatially explicit simulation models allow to make predictions incorporating multiple drivers that operate at broad spatiotemporal scales and making predictions under possible future scenarios. Both methodologies help the improvement of the study of insect pest and disturbance interaction and play an essential role in the management of landscape dynamics

References

Allen CD, Macalady AK, Chenchouni H, et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manag*e 259:660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Allstadt AJ, Haynes KJ, Liebhold AM, Johnson DM (2013) Long-term shifts in the cyclicity of outbreaks of a forest-defoliating insect. *Oecologia* 172:141–151. https://doi.org/10.1007/s00442-012-2474-x

Altmann SH (2013) Crown condition, water availability, insect damage and landscape features: Are they important to the Chilean tree Nothofagus glauca (Nothofagaceae) in the context of climate change? *Aust J Bot* 61:394–403. https://doi.org/10.1071/BT13015

Anderegg WRL, Allen CD, Hicke JA, et al (2015) Tree mortality from drought , insects , and their interactions in a changing climate. *New Phytol* 208:674–683. https://doi.org/10.1111/nph.13477

Barbet-Massin M, Rome Q, Villemant C, Courchamp F (2018) Can species distribution models really predict the expansion of invasive species? *PLoS One* 13:1–14. https://doi.org/10.1371/journal.pone.0193085

Bassols E, Oliveras J (2014) *Cydalima perspectalis* (Walker , 1859), una nova espècie invasora a Catalunya (Lepidoptera) *Butll Soc Cat Lep* 105:71–78

Battisti A, Stastny M, Buffo E, Larsson S (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Glob Chang Biol* 12:662–671. https://doi.org/10.1111/j.1365-2486.2006.01124.x

Blackburn TM, Essl F, Evans T, et al (2014) A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biol* 12:. https://doi.org/10.1371/journal.pbio.1001850

Blackburn TM, Pyšek P, Bacher S, et al (2011) A proposed unified framework for biological invasions. *Trends Ecol Evol* 26:333–339. https://doi.org/10.1016/j.tree.2011.03.023

Bouchard M, Aquilué N, Périé C, Lambert MC (2019) Tree species persistence under warming conditions: A key driver of forest response to climate change. *For Ecol Manage* 442:96–104. https://doi.org/10.1016/j.foreco.2019.03.040

Bradshaw CJA, Leroy B, Bellard C, et al (2016) Massive yet grossly underestimated global costs of invasive insects. *Nat Commun* 7:. https://doi.org/10.1038/ncomms12986

Cooke BJ, Lorenzetti F (2006) The dynamics of forest tent caterpillar outbreaks in Québec, Canada. *For Ecol Manage* 226:110–121. https://doi.org/10.1016/j.foreco.2006.01.034

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *TREE* 14:135–139. https://doi.org/https://doi.org/10.1016/S0169-5347(98)01554-7

Elith J, Graham CH (2009) Do they? How do they? WHY do they differ? on finding reasons for differing performances of species distribution models. *Ecography* (Cop) 32:66–77. https://doi.org/10.1111/j.1600-0587.2008.05505.x

Gallien L, Douzet R, Pratte S, et al (2012) Invasive species distribution models - how violating the equilibrium assumption can create new insights. *Glob Ecol Biogeogr* 21:1126–1136. https://doi.org/10.1111/j.1466-8238.2012.00768.x

Gallien L, Münkemüller T, Albert CH, et al (2010) Predicting potential distributions of invasive species: Where to go from here? *Divers Distrib* 16:331–342. https://doi.org/10.1111/j.1472-4642.2010.00652.x

Guisan A, Thuiller W, Zimmermann NE (2017) Habitat suitability and distribution models with applications in R. *Cambridge University Press*

Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. *Conserv Biol* 22:534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Herms D (2004) Using degree-days and plant phenology. In: *Minnesota Agricultural Experiment Station Publication*. pp 49–59

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *J Appl Ecol* 46:10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Jactel H, Koricheva J, Castagneyrol B (2019) Responses of forest insect pests to climate change: not so simple. *Curr Opin Insect Sci* 35:103–108. https://doi.org/10.1016/j.cois.2019.07.010

James PMA, Fortin MJ, Sturtevant BR, et al (2011) Modelling spatial interactions among fire, spruce budworm, and logging in the boreal forest. *Ecosystems* 14:60–75. https://doi.org/10.1007/s10021-010-9395-5

Kelsey RG, Gallego D, Sánchez-García FJ, Pajares J a. (2014) Ethanol accumulation during severe drought may signal tree vulnerability to detection and attack by bark beetles. *Can J For Res* 44:554–561. https://doi.org/10.1139/cjfr-2013-0428

Klutsch JG, Shamoun SF, Erbilgin N (2017) Drought stress leads to systemic induced susceptibility to a nectrotrophic fungus associated with mountain pine beetle in *Pinus banksiana* seedlings. *PLoS One* 12:. https://doi.org/10.7939/DVN

Meigs GW, Zald HSJ, Campbell JL, et al (2016) Do insect outbreaks reduce the severity of subsequent forest fires? *Environ Res Lett* 11:. https://doi.org/10.1088/1748-9326/11/4/045008

Myers JH, Cory JS (2013) Population cycles in forest lepidoptera revisited. *Annu Rev Ecol Evol Syst* 44:565–592. https://doi.org/10.1146/annurev-ecolsys-110512-135858

Nacambo S, Leuthardt FLG, Wan H, et al (2014) Development characteristics of the box-tree moth *Cydalima perspectalis* and its potential distribution in Europe. *J Appl Entomol* 138:14–26. https://doi.org/10.1111/jen.12078

Niinemets Ü, Valladares F (2006) Tolerence to shade, drought, and waterlogging of temperate northern hemisphere trees and shrub. *Ecol Monogr* 76:521–547

Pureswaran DS, Roques A, Battisti A (2018) Forest insects and climate change. *Curr For Reports* 4:35–50. https://doi.org/10.1007/s40725-018-0075-6

Pyšek P, Jarošík V, Hulme PE, et al (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proc Natl Acad Sci U S A* 107:12157–12162. https://doi.org/10.1073/pnas.1002314107

Robert LE, Sturtevant BR, Kneeshaw D, et al (2020) Forest landscape structure influences the cyclic-eruptive spatial dynamics of forest tent caterpillar outbreaks. *Ecosphere* 11:. https://doi.org/10.1002/ecs2.3096

Robinet C, Rousselet J, Roques A (2014) Potential spread of the pine processionary moth in France: Preliminary results from a simulation model and future challenges. *Ann For Sci* 71:149–160. https://doi.org/10.1007/s13595-013-0287-7

Suppo C, Bras A, Robinet C (2020) A temperature- and photoperiod-driven model reveals complex temporal population dynamics of the invasive box tree moth in Europe. *Ecol Modell* 432:. https://doi.org/10.1016/j.ecolmodel.2020.109229

Tenow O, Nilssen AC, Bylund H, et al (2013) Geometrid outbreak waves travel across Europe. *J Anim Ecol* 82:84–95. https://doi.org/10.1111/j.1365-2656.2012.02023.x

Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849. https://doi.org/10.1358/dot.2011.47.2.1576694

Uden DR, Allen CR, Angeler DG, et al (2015) Adaptive invasive species distribution models: a framework for modeling incipient invasions. *Biol Invasions* 17:2831–2850. https://doi.org/10.1007/s10530-015-0914-3

Vandermeer J (2006) Oscillating populations and biodiversity maintenance. *Bioscience* 56:967–975. https://doi.org/10.1641/0006-3568(2006)56[967:OPABM]2.0.CO;2

Wilson WG, Lundberg P, Vázquez DP, et al (2003) Biodiversity and species interactions: Extending Lotka-Volterra community theory. *Ecol Lett* 6:944–952. https://doi.org/10.1046/j.1461-0248.2003.00521.x