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Forest health under climate change: impact of insect pests

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The impact of climate change on forests is difficult to predict, as it depends on multiple factors and the final effect may vary in different parts of our planet. However, these effects can be sorted in “direct”, when they act directly on plants, and “indirect”, when they act through other agents. Among the indirect ones, there are those mediated by biotic factors, particularly insect pests. The impact of climate change on insect pests varies depending on the insect species and the type of forest. Some plant-feeding insects may be disfavoured by climate change, with a consequent reduction in population density and thus in damage to forests. However, many outbreaks of forest insects have been recently recorded as related to climate change. In fact, some insect pests, in certain regions of the world, may benefit from higher temperatures, as it has been demonstrated for some devastating defoliators. In addition, more frequent drought and extreme events may favour other pests, particularly bark beetles and wood-boring insects. Bark beetles are the most dangerous ones because their aggressiveness changes with population density. They can attack only stressed trees at low population densities, while, once the populations have reached high density, they are even able to attack healthy trees in widespread areas.

Keywords: Bark Beetles, Defoliators, Outbreaks, Voltinism

Introduction

Climate change may have positive or negative effects on forests, depending on local initial conditions (Allen et al. 2010). Positive effects are perceived for example by the so-called “energy-limited forests”. These are forests growing in cold climates, thus limited by a short growing season, like sub-alpine forests. In this case, a growing season that is prolonged by climate change and ensuing warmer temperatures, may positively affect tree growth (Vose et al. 2018). On the other hand, most forests are limited by water availability. In fact, water

is the main limiting factor for plant productivity all over our planet (Roebroek et al. 2020). In this type of forests, a warmer climate, associated with increased drought, has generally a negative effect on tree health (Vose et al. 2018). Hereafter, in this paper we will refer in particular to the forests of the temperate and boreal regions.

Although the negative effects of climate change are numerous, variable, and interacting with each other, they can be roughly distinguished into “direct” and “indirect”. As regards direct adverse effects on forest ecosystems, the acting factors are temperature, precipitation, wildfires, and extreme weather events. For example, higher temperatures and/or water stress have been identified as the most probable causes of increased tree mortality in southern European and western North American forests (Allen et al. 2010). Higher mortality is observed in different forest types, independently of tree size or plant genera (Daniels et al. 2011).

The increase in wind damage is another phenomenon caused by climate change (Pawlik & Harrison 2022). Windstorms represent one of the main abiotic disturbances in European forests and the main cause of forest damage (Pawlik & Harrison 2022). However, it is not clear if this increase in damage is due to higher storm frequency and intensity or to higher tree susceptibility. In fact, temperature and precipitation changes alter soil properties and it is sup-

posed that trees in these conditions are more prone to wind damage (Pawlik & Harrison 2022).

Finally, an increase in wildfires is also expected because of climate change (Seidl et al. 2017). In fact, due to warmer and drier climate conditions occurring in various regions of the globe, an increase in fire-prone areas is expected globally, particularly in temperate and boreal climates (Senande-Rivera et al. 2022). Furthermore, warmer seasons, as well as the lengthening of the potential fire season, and thus drier vegetation, cause an increment in the frequency and duration of burning fires (Westerling et al. 2006) and finally higher wildfire damage.

Indirect negative effects are to be added to the aforementioned direct ones. Climate stressors can have deleterious effects on tree vigour, acting through different mechanisms. For example, water stress reduces carbon availability leading to carbon starvation, which threatens plant survival (Allen et al. 2010). In addition, tree vigour can be reduced also through effects on their symbionts. In fact, although the impact of climate change on plant microbiota is poorly understood (Trivedi et al. 2022), it is hypothesized that climate stressors can alter the diversity and structure of microbial communities (Hernandez et al. 2021), possibly causing plant microbiota dysbiosis (Trivedi et al. 2022). In both cases the final effect is an increase in plant susceptibility to biotic factors (Allen et al. 2010, Vose et al.

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2018, Pureswaran et al. 2018), particularly pathogens and insect pests. However, since climate changes affect at the same time trees, insect pests, as well as their interactions, the combined effect is very complex and hardly predictable. As mentioned above, some warm-adapted insect pests can benefit from higher temperatures and drier climates (Engelhardt et al. 2022), leading to increased damage to forests. Conversely, other pest species may be negatively affected and, as a result, their population densities may decrease, ultimately leading to reduced forest damage (Netherer & Schopf 2010, Ramsfield et al. 2016).

Effect of insect pest response to climate change on forests

Climate change may alter the frequency and intensity of forest pest outbreaks (Volney & Fleming 2000), however, these effects may vary, as outbreaks can be enhanced or decreased by the changed climatic parameters (Lehmann et al. 2020). The response of insect pests, in fact, may depend on the intensity of climate stressors as well as on the insect species (Tab. 1). Effects on certain species are well studied, however, generalization is not possible, as each species reacts very differently to the changing climate (Pureswaran et al. 2018). In addition, the same species may have multiple and contrasting responses to climate change, in other words, its damage may increase or decrease according to the local community and geographical region (Lehmann et al. 2020, Harvey et al. 2023). Some species increase the outbreak intensity in the northern part of their range, while reducing it in the southern parts (Lehmann et al. 2020, Johnson & Haynes 2023). Many insects are shifting their range poleward and to higher elevations (Harvey et al. 2023). In addition, climate factors may act in different ways on insects, affecting their survival (directly or through the activity of their natural enemies), their life cycle, their dispersal capacity, their distribution, and their trophic interactions (Dale et al. 2001).

Negative impact of climate change on insect populations

Temperatures

Insects, being ectothermic organisms, are strongly affected by temperature. Each species has a specific temperature range within which finds the proper conditions to survive. Thus, summer higher temperatures linked to climate change may negatively affect insects. If the temperature increases above this range, adverse effects may occur, such as decreased individual size, fecundity, dispersal capacity, and increased mortality rates (Friedenberg et al. 2008, Wetherington et al. 2017, Jactel et al. 2019, Quandahor et al. 2023). Mild winter temperatures may affect insects differently. Certain insect species require chilling

periods to enter the obligate winter diapause, so the privation of these lowering temperatures may lead to higher mortality. In addition, higher winter temperatures lead to a snowfall decrease and an earlier snowmelt. This may negatively affect the survival of species that benefit from snow protection during overwintering in the soil (Netherer & Schopf 2010).

Insect-plant interactions

Changing climate may affect interactions between insect pests and their host plant. For example, due to climate change some specialist insects, strictly synchronized with host plant, may be negatively affected by a change in plant phenology. Some defoliators may have a short timeframe within which leaves provide proper quality food (Nanninga et al. 2023). Thus, if climate change acts differently on these species' phenology than on that of its host, a desynchronization may occur (Woods et al. 2010, Pureswaran et al. 2018). Lack of synchrony leads to a reduction in insect abundance (Battisti 2008, Ramsfield et al. 2016) and thus plant damage is also reduced.

Severe water stress, which is expected with climate change, can modify the content of primary and secondary metabolites in plants, reducing nitrogen and water content, and thus affecting plant-feeding insects (Harvey et al. 2023). Based on the most accepted hypothesis, the effects on insects depend on their feeding guild and the intensity of the stressors. Sap-sucking insects, as well as defoliators and leaf-mining insects, for example, are negatively affected by severe droughts as the weather-stressed host offers them low-quality food (Netherer & Schopf 2010, Gely et al. 2020, Harvey et al. 2023).

Natural enemies

Finally, since the insect pest density also depends on natural control agents, the responses of their natural enemies to climate change should be considered. Effects are not easily predicted and authors have contrasting opinions about them. Some researchers argue that a warming climate can be more deleterious on predators or parasitoids than on their prey or hosts, with beneficial effects on pest populations (Wetherington et al. 2017, Harvey et al. 2023). Conversely, others think that reduced food quality for insect pests, with the resulting lengthening of their life cycle, exposes them for longer periods to their natural enemies (Skirvin et al. 1997, Netherer & Schopf 2010). Based on this last theory, pest population densities would be reduced by climate change.

In conclusion, some insect pests may be negatively impacted by climate change, either directly, with effects on their survival or performances, or indirectly, through changes in host plant phenology or their natural enemies' performance. This kind of effect may lead to a reduction in the population density of insect pests and in some

cases to their range contraction (Lehmann et al. 2020, Harvey et al. 2023), with a consequent reduction of damage to forests.

Positive impact of climate change on insect populations

Temperatures

Warmer climate may favour some insect pests, particularly in regions where their optimal temperatures are not reached. Insect development rates strictly depend on temperatures: it is faster at optimal temperatures, while it slows down at suboptimal temperatures, regardless of them being higher or lower. Each species has a different sensibility to temperatures and a different optimal level. Some insect pests may be favoured in some regions, particularly those at higher latitudes, where temperatures are lower than their optimal level (Lehmann et al. 2020). Here, an increase in temperatures would accelerate their metabolic rate, thus increasing their development and movement capability, as well as reducing their mortality, ultimately leading to an increase in population density (Dukes et al. 2009, Jaworski & Hilszczanski 2013, Zhou et al. 2017).

A higher development rate leads to shorter life cycles and, for multivoltine species, to a higher number of generations per year. This is also enabled by an extended growing season, which generally occurs due to climate change (Lange et al. 2006, Jönsson et al. 2009, Jaworski & Hilszczanski 2013, Harvey et al. 2023). Therefore, clearly, if an insect pest has more generations per year, the damage it causes to plants increases too (Jaworski & Hilszczanski 2013).

In addition, in areas where winter low temperatures are a limiting factor for insects, an increase in temperatures may reduce mortality rates of insects without an obligate winter diapause (Dukes et al. 2009). This was demonstrated both for species that overwinter as eggs and those overwintering as larvae. Some examples are forest defoliators like the winter moth *Operophtera brumata* L., the gypsy moth *Lymantria dispar* (L.), and the European pine sawfly *Neodiprion sertifer* (Geoffroy), whose egg mortality rates have been reduced by higher winter temperatures (Veteli et al. 2005, Jepsen et al. 2008, Netherer & Schopf 2010). In the case of defoliators which overwinter as larvae the effect is more complex. One of the most studied cases is that of a Mediterranean species, namely the pine processionary moth, *Thaumetopoea pityocampa* (Denis et Schiffermüller). Its larvae actively feed during winter if temperatures allow it. This winter feeding reduces overwintering mortality and increases insect performances, leading to an increase in females' fecundity (Battisti et al. 2005, Battisti 2008, Tiberi et al. 2015).

With the warming climate, many insect pests are expanding their distribution and

Tab. 1 - Examples of negative and positive effects on insects of various abiotic factors involved in climate change. Impact: Impact of climate change on insect populations; (*): Mechanism by which the effect on the insect population is achieved.

Impact	Feeding guild	Abiotic factor	Insect species	Acting mechanism (*)	References
Negative impact	Sapsucking insects	Water stress	<i>Adelges abietis</i>	Higher plant resistance	Quandahor et al. 2023
		Higher temperatures	Aphids	Increase in coccinellid predators	Skirvin et al. 1997
	Defoliators	Water stress	<i>Operophtera brumata</i>	Reduction in food quality	Jactel et al. 2019
		Higher winter temperatures	<i>Zeiraphera diniana</i>	Diapause disruption	Battisti 2008
		Warmer spring temperatures		Desynchronization with host plant	Battisti 2008
	Xylophagous insects	Higher temperatures (above the optimum)	<i>Dendroctonus frontalis</i>	Decline of population growth	Friedenberg et al. 2008
Higher temperatures		<i>Agrilus planipennis</i>	Shorter oviposition period	Wetherington et al. 2017	
Positive impact	Sapsucking insects	Higher temperatures	<i>Phenacoccus solenopsis</i>	Higher growth rate and better tending by ants	Zhou et al. 2017
	Defoliators	Higher temperatures	<i>Cephalcia arvensis</i>	Higher larval survival and faster development	Battisti 2008
			<i>Lymantria monacha</i> and <i>Lymantria dispar</i>	Higher larval survival and faster development	Jaworski & Hilszczanski 2013
		Higher winter temperatures	<i>Lymantria dispar</i>	higher winter survival of eggs	Netherer & Schopf 2010
			<i>Neodiprion sertifer</i>	higher winter survival of eggs	Veteli et al. 2005
			<i>Operophtera brumata</i>	higher winter survival of eggs	Jepsen et al. 2008
			<i>Thaumetopoea pityocampa</i>	Higher overwintering survival, higher females' fecundity, increase in distribution range and outbreak areas	Battisti 2008, Battisti et al. 2005, Tiberi et al. 2015
	Xylophagous insects	Higher temperatures	<i>Agrilus planipennis</i>	Reduction in mortality by parasitoids	Wetherington et al. 2017
			<i>Dendroctonus ponderosae</i>	Increase in distribution range and outbreak areas	Logan & Powell 2009
			<i>Ips typographus</i>	Faster larval development and more generations per year	Lange et al. 2006, Jönsson et al. 2009
		Water stress	<i>Dendroctonus</i> spp.	Higher tree susceptibility	Guarín & Taylor 2005,
			<i>Tomicus piniperda</i> and <i>Tomicus minor</i>	Higher tree susceptibility	Krams et al. 2012
		Windstorms	<i>Ips typographus</i>	Higher tree susceptibility	Marini et al. 2017, Nikolov et al. 2015, Nardi et al. 2022
Wildfires		<i>Dendroctonus</i> spp. and <i>Ips</i> spp.	Higher tree susceptibility	McHugh et al. 2003, Hood & Varner 2019	
	<i>Ips pini</i>	Higher tree susceptibility	Santoro et al. 2001, Hood & Varner 2019		

outbreak areas in regions that previously exceeded their thermal tolerance. In these new environments, they may have a higher impact due to the lack of coevolution, with higher damage to plants. This has been confirmed for many species of bark beetles and defoliators, which have recently increased their performances at higher elevations (Pureswaran et al. 2018). Again *T. pityocampae* may serve as an example, as its outbreaks have been recently reported beyond both the northern and the altitude limits of its historical occurrence (Battisti 2008).

Insect-plant interactions

The multiple negative effects of climate change make forest trees prone to pest attacks. Adverse effects of warm temperatures and drought reduce plant defences, making them susceptible to pests. Indeed, while sap-sucking insects and defoliators

may be negatively affected by severe droughts, generally, xylophagous insects benefit from them (Pureswaran et al. 2018, Netherer & Schopf 2010, Gely et al. 2020, Harvey et al. 2023, Vacek et al. 2023). In fact, many outbreaks of bark beetles have recently been reported after drought events. The main species involved in this phenomenon belong to the *Tomicus*, *Ips*, and *Dendroctonus* genera (Guarín & Taylor 2005, Allen et al. 2010, Krams et al. 2012).

Finally, outbreaks by bark beetles and wood boring insects can be triggered by increasingly frequent windstorm and wildfire disturbances. As a result of these events abundant breeding material is made available for those insect species that exploit felled and broken trees, partially burned trees, and stressed trees in general. This kind of material is suitable for pest colonization, causing the population to build up rapidly (Santoro et al. 2001, McHugh et al.

2003, Hood & Varner 2019, Seidl et al. 2017, Jactel et al. 2019). Especially for bark beetles, this situation is even more complex because their aggressiveness changes with population density. Once the population has reached high density the pest is even able to attack healthy trees, not only stressed ones (Marini et al. 2017). Initially, this occurs in single "spots", near weakened trees, then on multiple spots, and finally in widespread areas (Schowalter 2012).

An example is the European spruce bark beetle, *Ips typographus* (L.) which has caused severe outbreaks after windstorms in Europe on various occasions (Nikolov et al. 2015, Marini et al. 2017). The more recent one is the "Vaia" storm occurred in the Alps in 2018, which has caused a huge infestation (still in progress) in the Italian spruce forests, even without the contribution of other climatic stressors (Nardi et al.

2022).

Although adverse effects on insect pests are possible, many outbreaks of forest insects have been related to climate change (Allen et al. 2010, Pureswaran et al. 2018). In fact, outbreaks of many insect pests, mainly bark beetles and defoliators, have been recorded in different areas of the world after extreme droughts. For example, the outbreaks of the two aggressive bark beetles *Dendroctonus ponderosae* Hopkins and *I. typographus* were associated to higher availability of trees stressed by droughts or to faster biological cycles favoured by higher temperatures (Guarín & Taylor 2005, Lange et al. 2006, Jönsson et al. 2009). Similarly, favourable climate promoted the survival and speeded up the development of some main forest defoliators, like the web-spinning sawfly *Cephalcia arvensis* Panzer (Battisti 2008). To these, we may add the aforementioned bark beetle outbreaks recorded after large and more frequent windstorms and wildfires (Nikolov et al. 2015, Marini et al. 2017, Nardi et al. 2022).

Conclusions

The impact of climate change on forests is difficult to predict, particularly when it is mediated by insect pests, as it can vary depending on various factors (Jactel et al. 2019). In any case, many outbreaks of forest insects have been recently recorded as related to climate change (Battisti 2008, Dukes et al. 2009, Logan & Powell 2009, Ramsfield et al. 2016). Generalisation is not possible, as many studies agree that insects belonging to different feeding guilds have different reactions to climate change. While the majority of sapsuckers and defoliators may be negatively affected by severe drought (Pureswaran et al. 2018, Hamann et al. 2021, Harvey et al. 2023), they may benefit from higher temperatures, if these do not exceed their optimal threshold (Netherer & Schopf 2010, Jactel et al. 2019). On the contrary, bark beetles and wood-boring insects generally benefit from both types of climate modifications (Guarín & Taylor 2005, Lange et al. 2006, Logan & Powell 2009, Krams et al. 2012); furthermore, they may be favoured by the occurrence of wildfires and extreme windthrows (Marini et al. 2017, Seidl et al. 2017, Jactel et al. 2019). Anyway, the impact of insect pests varies depending on the insect species and the type of forest, in addition, the same insect species may decrease or increase both outbreak frequency and intensity in the different regions of its distribution range (Lehmann et al. 2020, Harvey et al. 2023, Johnson & Haynes 2023).

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