Henrik Hartmann[1,2,3], Andrea Battisti[13], Eckehard G. Brockerhoff[9], Marta Bełka[4], Rainer Hurling[5], Hervé Jactel[6], Jonàs Oliva[7,8], Jerome Rousselet[14], Eeva Terhonen[10], Tiina Ylioja[10], Markus Melin[10], Åke Olson[11], Freja De Prins[11], Ke Zhang[11], Matilda Stein Åslund[11], Kateryna Davydenko[11], Audrius Menkis[11], Malin Elfstrand[11], Milan Zúbrik[15], Andrej Kunca[15], Juraj Galko[15], Márton Paulin[16], György Csóka[16], Gernot Hoch[12], Milan Pernek[17], Sebastian Preidl[1], Rico Fischer[1]

European forests are under increasing pressure from global change-driven invasions and accelerating epidemics by insects and diseases

Europäische Wälder stehen unter zunehmendem Druck durch die durch globalen Wandel bedingte Zunahme von Invasionen und Epidemien durch Insekten und Krankheiten

Affiliations
[1]Julius Kühn Institute (JKI) – Federal Research Centre for Cultivated Plants, Institute for Forest Protection, Quedlinburg, Germany.
[2]Georg August University, Faculty of Forest Sciences and Forest Ecology, Göttingen, Germany.
[3]Max Planck Institute for Biogeochemistry, Department of Biogeochemical Processes, Jena, Germany.
[4]Poznań University of Life Sciences, Forest Entomology and Pathology Department, Faculty of Forestry and Wood Technology, Poznań, Poland.
[5]Northwest Forest Research Institute (NW-FVA), Department of Forest Protection, Göttingen, Germany.
[6]University of Bordeaux, INRAE, Biogeco, Cestas, France.
[7]University of Lleida, Department of Agricultural and Forest Sciences and Engineering, Lleida, Spain.
[8]Joint Research Unit CTFC–AGROTECNIO-CERCA, Lleida, Spain.
[9]Swiss Federal Research Institute WSL, Forest Health and Biotic Interactions, Birmensdorf, Switzerland.
[10]Natural Resources Institute Finland (Luke), Forest health and biodiversity, Helsinki, Finland.
[11]Swedish University of Agricultural Sciences, Department of Forest Mycology and Plant Pathology, Uppsala, Sweden.
[12]BFW – Austrian Research Centre for Forest, Department of Forest Protection, Vienna, Austria.
[13]University of Padova, Department DAFNAE, Legnaro, Italy.
[14]INRAE, Unité Zoologie forestière, Ardon, Orleans, France.
[15]National Forest Centre, Forest Protection Service, Banská Štiavnica, Slovakia.
[16]University of Sopron, Forest Research Institute, Department of Forest Protection, Mátrafüred, Hungary.
[17]Croatian Forest Research Institute, Division of Forest Protection and Game Management, Jastrebarsko, Croatia.

Correspondence
Prof. Dr. Henrik Hartmann, Julius Kühn Institute (JKI) – Federal Research Centre for Cultivated Plants, Institute for Forest Protection, Erwin-Baur-Straße 27, 06484 Quedlinburg, Germany, email: henrik.hartmann@julius-kuehn.de

Abstract

Rising temperatures attributed to anthropogenic climate change have held a firm grip on European forests for over two decades now and disturbances have increased substantially, mainly from insects and pathogens. Empirical evidence suggests a direct linkage between rising temperatures and increasing damage from native insects. Although the rapid spread of non-native invasive pests and pathogens is mainly driven by globalized trade and lacking tree species adaptation to locally new threats, climate change favors rapid range expansion of some invasive pests. Here, we present some examples of tree-insect-pathogen interactions in native and non-native systems that have experienced climate change-induced severe outbreak dynamics. We document the spread of damaging insects and pathogens into previously climatically unsuitable regions and underscore the severe forest damages such species distribution shifts can cause. Although systematic assessments are still pending, the information provided here by multiple independent empirical evidences is highly valuable for identifying some of the most pressing issues in European forest protection. Our work can guide forest protection agencies in preparing mitigating strategies for upcoming decades.

Keywords

forest health, forest decline, forest protection, climate change

Zusammenfassung

Der Klimawandel hat die europäischen Wälder seit mehr als zwei Jahrzehnten fest im Griff, und Störungen, vor allem durch Insekten und Krankheitserreger, haben erheblich zugenommen. Untersuchungen deuten auf einen direkten Zusammenhang zwischen steigenden Temperaturen und zunehmenden Schäden durch einheimische Insekten hin. Obwohl die rasche Ausbreitung nicht-einheimischer invasiver Schädlinge und Krankheitserreger hauptsächlich durch den globalisierten Handel und die mangelnde Anpassung der Baumarten an neue Bedrohungen bedingt ist, begünstigt der Klimawandel auch die rasche Ausbreitung einiger invasiver Schädlinge. In diesem Artikel stellen wir Beispiele von Baum-Insekten-Pa-

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thogen-Systemen vor, die durch den Klimawandel eine starke Verstärkung der Ausbruchsdynamik erfahren haben. Wir dokumentieren die Ausbreitung von Schadinsekten und Krankheitserregern in zuvor klimatisch ungeeignete Regionen und die durch solche Artenverschiebungen verursachten Schäden. Obwohl eine systematische Erfassung dieser Ereignisse noch aussteht, sind die hier von erfahrenen Wissenschaftlern zusammengetragenen Informationen sehr wertvoll, einige der dringendsten Probleme des europäischen Waldschutzes aufzuzeigen.

Stichwörter

Waldgesundheit, Waldsterben, Waldschutz, Klimawandel

Introduction: climate change and its impact on interactions between forest insects and pathogens

Global warming, heat waves and extended drought have a firm grip on the European continent for more than two decades now. For Central Europe, the hot and dry summers of 2018–19 brought upon conditions that had not been observed since the beginning of weather recordings (C3S, 2019). In 2018, the lowest annual soil moisture during the last 40 years occurred across much of Central Europe, along with an average annual temperature among the three highest on record. Ten of the warmest years on record occurred since 2007, including the three warmest since 2020 (C3S, 2024). During the same period, forest disturbances have increased substantially throughout Europe (Patacca et al., 2023; Senf & Seidl, 2021), mainly from insects and pathogens, but also due to an increase in forest fires (Forzieri et al., 2021). Satellite data collected for more than 40 years suggest a direct linkage between rising temperatures and increasing insect damages and, with ongoing climate change, further severe and more frequent large-scale biotic forest damage has to be expected (Forzieri et al., 2021). Within a few years, more than 500,000 hectares of forest had been damaged by biotic agents in Germany alone, with bark beetle outbreaks being a main cause since 2018 (Thonfeld et al., 2022). The rapid spread of non-native invasive pests and pathogens, such as the invasive fungal pathogen that causes ash dieback, is mainly a result of increasing globalized trade and the lack of adapted defenses of established tree species (Brockerhoff et al., 2014), however, some invasive species also benefit from climate change with rapid range expansion (Hulme, 2017).

Damaging forest insects, but also tree pathogens, are an integral driver of natural forest ecosystem dynamics, and typically attack trees of low vigor and accelerate tree health decline and tree death (Franklin et al., 1987; Manion, 1991). Standing dead trees provide habitat for many bird species, arthropods or fungi, and are thus important factors for maintaining forest biodiversity (Stokland et al., 2012). Fallen dead trees continue playing crucial ecological roles as coarse woody debris by providing shelter and habitat for many forest plant, animal and fungal species, as slow-release reservoirs in nutrient cycling, but also as favorable sites for seed germination, seedling establishment and tree species regeneration, often referred to as nurse logs (Woods et al., 2021). By creating habitat trees and nurse logs, damaging forest insects and tree pathogens play an important role in processes related to forest resilience or succession. However, large-scale tree mortality which may lead to area-wide temporary or longer-term loss of forest vitality and reduced forest resilience (Forzieri et al., 2022), is detrimental for forest biodiversity, especially when impacts of disturbances are exacerbated by salvage logging (e.g., Basile et al., 2023).

Climate warming and climate extremes are unbalancing the natural tree-insect-pathogen systems via opposing effects on tree and insect/pathogen physiology (Fig. 1). Elevated temperature and severe water shortage reduce tree carbon uptake and increase carbon loss via respiration, which results in a negative carbon balance and thus resource shortage for maintaining tree defenses (McDowell, 2011). At the same time, elevated temperatures accelerate physiological processes in ectothermic organisms like insects or bacteria and thus increase reproductive rates and development. For example, the development time of the European spruce bark beetle (*Ips typographus*) from egg to adult beetle is more than twice as fast at 25 °C than at 15 °C (Wermelinger & Seifert, 1999). Consequently, the reproductive cycles accelerate at elevated temperatures, allowing more generations of beetles to develop within a growing season (Jakoby et al., 2019). Given that population sizes can increase 15-fold from one generation to the next under favorable conditions (Hlásny et al., 2019), each additional generation of beetles increases herbivore pressure at an exponential rate. This allows beetles to successfully attack and kill trees weakened by heat and drought stress, or storm damage (Stadelmann et al., 2014), and at high enough number even healthy trees (Hlásny et al., 2019), which can lead to substantial forest damage like total canopy cover loss (Fig. 1). Elevated temperatures beyond a certain threshold can also have negative effects on pest development and survival, so far however, thresholds of heat tolerance have been defined mainly in controlled laboratory or greenhouse studies (Frank, 2021), making inferences on tipping points in real forests highly uncertain.

In addition to the threats from unbalanced native tree-insect/pathogen-systems, new threats originate from introduced pests and diseases, sometimes equally exacerbated by changing climatic conditions, and many of the new introduced species have the potential to seriously harm European forests or have already done so. Invasion of European forests by non-native forest insects and pathogens has been occurring at an increasing and alarming rate during the last decades (Roques et al., 2020; Santini et al., 2013), mainly as a result of globalized international trade (Schuler et al., 2023). A few of these new threats have already been identified in Europe; some of them are spreading at enormous speed through their new habitats and causing severe forest damages, as we will show in the following sections. Other species are spreading increasingly into non-native regions and, if they have not yet been detected in Europe, their establishment in the future is very likely (Seebens et al., 2017). These new threats can be exacerbated by various factors, including management-induced changes in forest structure and composition at ecosystem or land-

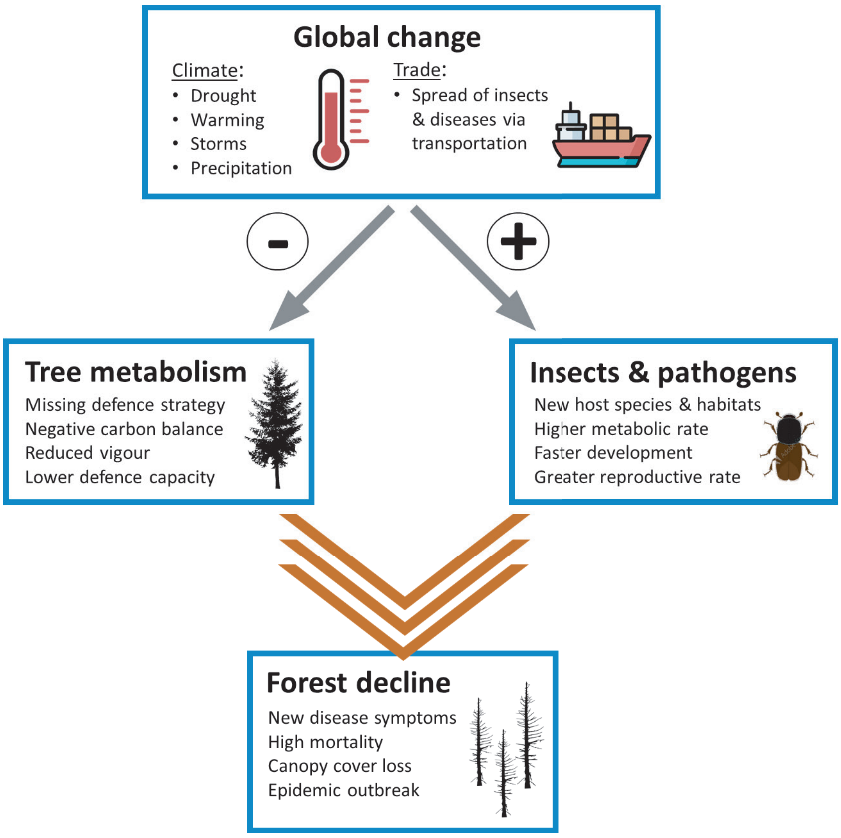

Fig. 1: Diverse effects of global change phenomena (climate and globalized trade) on tree metabolism and on insect and tree pathogens development and reproduction and spread of non-native insects and diseases. Reduced tree vitality and ensuing low defense capacity collides with faster development and greater reproductive rates of insects and diseases, or colonization of trees by non-native insects and diseases for which host species have no defensive strategy. This leads to disease and epidemic outbreak symptoms in forests, like high mortality rates and canopy cover loss. Because climate change continues to act on these systems, recovery to the original state is highly uncertain. Icons by https://www.freepik.com/ and https://BioRender.com.

scape scales; however, climate change also influences interactions between trees and introduced insects/pathogens and thus contributes to greater host susceptibility to colonization or infection. While several invasions have been successfully eradicated and not all invasions are imposing significant negative impacts on the newly colonized ecosystems (Avtzis et al., 2019), there are several alien pests and pathogens that do pose severe threats to the ecological integrity of forests and can cause considerable economic losses (Brockerhoff et al., 2006).

In this paper, we present some examples of native tree-insect-pathogen systems that have experienced climate change-induced severe outbreak dynamics, we will report instances of damaging insects and pathogens spreading into new regions that have previously been climatically unsuitable for them, and document the severe damages that this species distribution shifts are causing. We highlight observations made by a large group of forest researchers across Europe. Our viewpoint article is not intended to provide a comprehensive overview of the forest health situation in Europe, but to indicate an alarming trend of native and introduced insects and pathogens taking hold of forest ecosystems with escalating speed and intensity. We include in our report personal assessments by the contributing researchers, even though some of their observations have not been empirically evaluated yet. In times of rapid climate change, processes in nature unfold faster than science can produce insights and solutions, although modeling and extrapolation of emerging trends are helpful. However, personal assessments of experienced researchers are a highly valuable source of information that can guide the scientific community to focus on key aspects of biotic interactions required to enhance our capacity to observe, understand, and predict forest pest dynamics. Such a scientific approach is badly needed to support policy and decision makers in defining the most pressing issues to be addressed in European forest protection management. Note that expert statements are deliberately intended as a call for awareness of how crucial measures against further climate change are for maintaining one important foundation of societal well-being – vital forests for our and for future generations.

Movement of pests towards latitudinal and altitudinal tree lines

Climate change-induced warming affects also regions at high altitudes and northern latitudes where low temperatures and short growing seasons so far have prevented severe outbreaks in forests in the past. In high latitudinal forests, climate warming is expected to facilitate northward movement of forests and increase tree growth rates (e.g., Liu et al., 2020). Here we present evidence that, despite the apparent improvement in general forest vitality, damaging insects or pathogens are putting these forests now under unprecedented and severe pressure.

Bark beetles are moving up to high altitude spruce forests

The European spruce bark beetle, *Ips typographus*, caused massive damage in Central European Norway spruce forests during the last decade. In most cases, outbreaks occurred in spruce forests at elevations below 700 m (where Norway spruce was planted and would not occur naturally) and with below-average precipitation (Marini et al., 2017). Many of these forests have large proportions of spruce, often originating from management activities like tree planting or stand structural homogenization, which make them highly vulnerable to bark beetle outbreaks and susceptible to severed damage. In the Czech Republic, salvage logging in lowland spruce forests peaked in 2019 with 23 million m^3 of dead or dying trees, while in northern Austria peak damage was 4.7 million m^3 in 2019. In both instances, drought was identified as the triggering element of the outbreak (Hallas et al., 2024; Hlásny et al., 2021). In Switzerland, spruce bark beetle outbreaks also peaked in 2019 with about 1.5 million m^3g beetle-killed timber (Stroheker et al., 2024), whereby the storm 'Burglind' in January 2018 and the droughts of 2018–2019, along with elevated temperatures, are considered the main trigger and drivers.

In the Southern Alps, a new outbreak started in 2021 and mortality of Norway spruce reached unprecedented levels in the southernmost parts of Austria and the Italian regions of Trentino-Südtirol and Veneto. This time, however, mountain forests way above 700 m elevation were affected, and – damage occurred even up to the upper limit of spruce distribution at around 1900 m a.s.l. In southern Austria, damaged volume reached 1.8 million m^3 in 2023, which far exceeds previous records in the affected region (Fig. 2 A), while on the Italian side the total beetle damage assessed so far amounts to 16 million ha. This bark beetle outbreak was preceded by extreme storm damage that occurred in autumn 2018, followed by two winters with very high snow damage. This situation provided easily accessible breeding material for spruce bark beetles, allowing populations to build up quickly and transition from endemic to the epidemic phases (Hlásny et al., 2019). The elevated temperatures of the recent years allowed successful development of two generations of spruce bark beetles at elevations up to at least 1400 m a.s.l. (Hallas et al., 2024), again an unprecedented phenomenon. With more than one generation of beetles developing per year, population growth increases exponentially and allows a faster transition from endemic to epidemic phases (Biedermann et al., 2019; Jakoby et al., 2019). This likely had been the driving force behind the extreme outbreak that started in 2021 and continued until 2023.

Mortality of Norway spruce from bark beetle outbreaks has a major impact in the affected mountain regions, typically characterized by very steep slopes. The loss of mature tree cover has significant socio-economic consequences, since many of these forests provide an important protection against natural hazards such as avalanches, rockfall, landslides, or flooding. Based on remote sensing tools (e.g., Löw & Koukal, 2020), more than one third of all protection forests have been lost in the most affected regions in Austria since the storm event in 2018. Costly technical measures in addition to high efforts into reforestation are required to protect people and infrastructure. Yet, ongoing climate change may cause further pressure from damaging insects on European forests (Forzieri et al., 2021) and it is uncertain whether reforestation efforts with currently native tree species will prove successful in the next decades (Wessely et al., 2024).

Large outbreaks of the European spruce bark beetle are not unusual in spruce dominated forests, but the ongoing outbreak in the Southern Alps adds a new aspect. Extent of damage and the dynamic of the outbreak have been beyond my imagination – despite 30 years' experience as forest entomologist. Now, all the safe zones are gone, stands are killed from the valleys up to the tree line. Steep slopes are denuded of their forest cover leaving many regions without protection against natural hazards and erosion. Elevated temperatures from climate change now allow several bark beetle generations to develop per year also at high elevations making available management options for bark beetle control fail in such situations.

Gernot Hoch, Austria

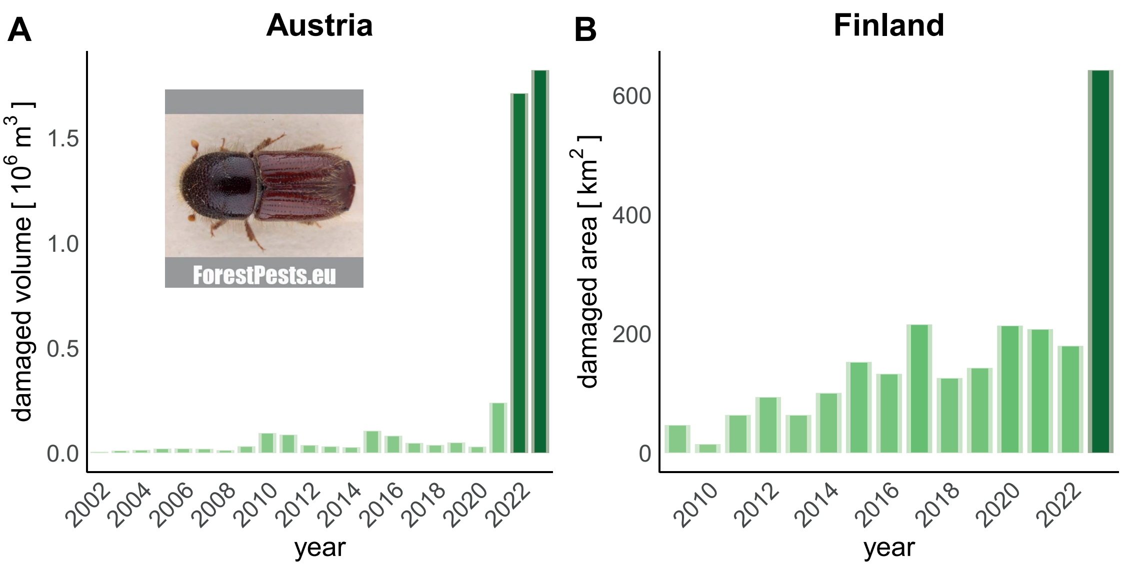

Fig. 2: Annual forest damage by European spruce bark beetle (*I. typographus*) in (A) three Southern Austrian Alps forest districts (in millions of m3) and (B) Finland (in km^2). Inlet: Photo of the European spruce bark beetle (ForestPests.eu, photo by M. Zúbrik). Data: Austria: Documentation of Forest Damaging Factors based on records from national Austrian forest authorities (https://www.bfw.gv.at/dokumentation-waldschaedigungsfaktoren/, data available on request). Finland: Data taken from the Finnish National Forest Inventory (Korhonen et al., 2021).

Bark beetles are spreading into northern latitudes

Finland´s forests have been relatively safe from large-scale epidemic insect damage, and many of the severe defoliators of Central Europe have not been present at high densities in the past. The situation has, however, been steadily changing due to the slow but gradual lengthening of the growing season, increases in annual temperatures, and the occurrence of unprecedented drought and heat events since the early 2020´s (Aalto et al., 2022; Venäläinen et al., 2020). These changes in climatic conditions have initiated range expansions of new forest pest species and caused new and locally dramatic levels of forest damage in many Finnish regions. For example, the spruce bark beetle has always been a part of Fennoscandians native fauna, re-colonizing the post-glacial Fennoscandia alongside with its main host, Norway spruce (Mayer et al., 2015). Locally confined damages, typically following storms, have been common in Southern Finland, but up to the 1900s only to a relatively small extent (Tikkanen & Lehtonen, 2023). Since then, the damaging potential of the species has increased with climate warming and more frequent occurrences of extreme weather events. Recent observations in Finland reach as high as 69° northern latitude. The drought-heat events of the early 2020s have triggered local forest damages as far up north beyond 65°, and caused a substantial 3-fold increase in affected area in 2023 (Pulgarin Diaz et al., 2024; Ylioja et al., 2024) , along with a steady gradual increase in forest area damaged by the spruce bark beetle (Korhonen et al., 2021). The increase in bark beetle-related salvage loggings in 2011 was triggered by the "Asta-Veera" storm events of 2010, whereas the peak in 2023 has occurred following the drought events of 2021 and 2022 (Fig. 2 B).

Northern movement of the nun moth and of pine shoot blight

The nun moth (*Lymantria monacha*) is another example of a range-expanding native forest pest. Between the 1950s and 1990s, the species was only occasionally encountered in Finland, but has moved northwards by at least 200 km since the late 1990s (Fält-Nardmann et al., 2018; Melin et al. 2020) and locally confined but severe damage events with high tree mortality have been recorded in Norway spruce trees (Heino & Pouttu, 2015). Pheromone surveys of the species document a steady northward expansion (Fig. 3) with a slow but continuous population growth, in particular at the northern edges of expansion (Melin et al., 2020). While current damage levels are not severe in the newly colonized regions, future warming is likely to cause further population growth of the insect also in these regions, which can be expected to increase risk of defoliation on the forests of the northern distribution ranges.

Diplodia sapinea shoot blight represents one of the best-documented examples of climate driven latitudinal expansions of a forest pathogen. *D. sapinea* is a facultative pathogen that causes disease when pine (Pinus) trees are subjected to stress and often reaches outbreak levels after hailstorm (Caballol et al., 2022) or drought events (Brodde et al., 2023b). *Diplodia sapinea* can be present as endophyte without causing harm to trees (Blumenstein et al., 2022), but once shoot dieback sets in, trees may die during a single growing season, if additional stress like drought or crown damage > 70% co-occur (Brodde et al., 2023b). Until recently, *D. sapinea* was known as a rare pathogen in alpine areas and entirely absent

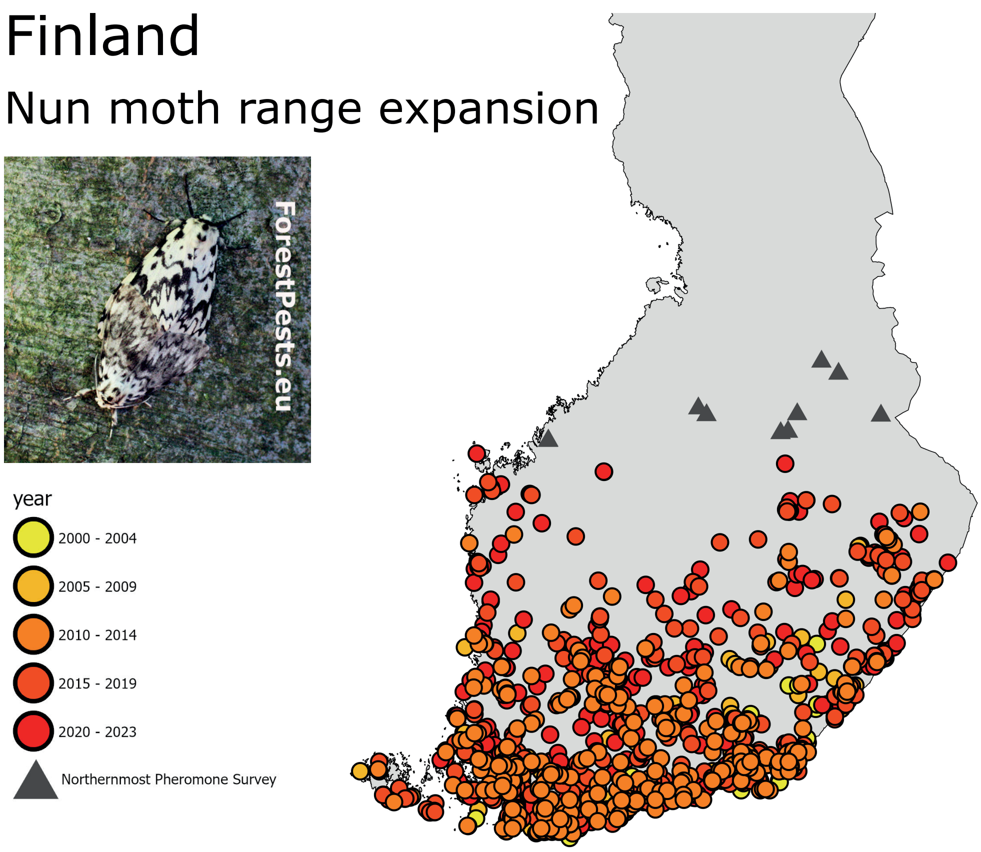

Fig. 3: Nun moth range expansion compiled from data of the Finnish Biodiversity Information Facility and the pheromone monitoring program of Natural Resources Institute Finland (described in Melin et al., 2020). Inlet: Mating on a tree trunk. Up female, down male. Photo: A. Kunca.

in northern latitudes. This situation has changed dramatically during the early 2000s and with accelerated warming. Northern Scots pine populations are physiologically not adapted to the new climate conditions, which make them more susceptible to the increased virulence of the pathogen (from latent to pathogenic), or the spread of new and more aggressive strains into previously unaffected regions.

First observations of the pathogen in Northern Europe were reported from Estonia in 2007, where it was detected on Austrian pine (*Pinus nigra* Arn.) (Hanso & Drenkhan, 2009). Then, in 2012, it was also discovered in native Scots pine forests in Estonia (Adamson et al., 2015), in 2013 on Scots pine cones in central Sweden and, in the same year, tip blight symptoms were discovered on three Austrian pines in southern Sweden (Oliva et al., 2013). In 2016, observations culminated in a large outbreak of *Diplodia* shoot blight near Stockholm (Brodde et al., 2019) and two years later, an unprecedented dieback from *D. sapinea* affected the island of Gotland (Brodde et al., 2023a). Further north in Finland, *D. sapinea* was first detected in 2015 on Scots pine cones (Müller et al., 2019), and tip blight symptoms have been recorded recently in 2021 (Terhonen, 2022). The northernmost occurrence of *D. sapinea* in Finland has been reported at 61°N (Terhonen et al., 2021); in Sweden, at 59.5°N (Brodde et al., 2019). This newly observed latitudinal expansion may have a large toll on Scots pine (*Pinus sylvestris*), a highly susceptible pine that is now exposed to the new emerging pathogen (Caballol et al., 2022).

Expansion of the pine processionary moth in Central Europe

The pine processionary moth (*Thaumetopoea pityocampa*) is a well-known forest insect pest of pines and cedars and, because of its urticating hairs, it can represent a threat to human and animal health. The processionary moth has recently been defined by the IPCC as an indicator species for climate warming (Roques, 2015) because of its dramatic range expansion. Higher winter temperatures and sustained higher summer night temperatures cause greater overwintering insect survival and allow longer flight distances of mated females (Battisti et al., 2006; Battisti et al., 2005; Robinet et al., 2012), which in combination lead to a rapid increase in population sizes and spread (Fig. 4). The insect has reached up into high elevation mountainous regions by about 400 m in the last 25 years in the Southern Alps and into northern latitudes of Central Europe by about 120 km in the last 25 years in central France (Fig. 4). In the period 1969–2021, this corresponds to a latitudinal expansion of 2–3 km/yr, depending on the weather of each year. In the mountains, an annual elevational shift of 5–10 m/yr has been observed, with larger upward jumps in warmer years (Battisti et al., 2006).

Forest ecosystems and human societies are now exposed to a new challenge with even a larger impact than in the core areas of the geographic range of *T. pityocampa*. Both the slow tracking by natural enemies and the lack of knowledge in human populations about how to address the threats by the new invader explain why the insect has a greater impact in the newly colonized regions (Roques, 2015). Heat islands in large cities are clearly facilitating its expansion into urban forests with often-problematic encounters with people and pets (Backe et al., 2021). The management of this pest is difficult and needs adaptation to each local condition because the insect may show periods of activity that differ from site to site, even on a small scale (Santos et al., 2011). Managers and policy makers should pay attention about the presence of the insect in order to adopt the most appropriate management options and to inform the public about the risks associated with the accidental exposure to the urticating hairs (Battisti et al., 2017). Given the climate forecast for Europe further expansion of pine processionary moth, both in elevation and latitude and in regions where its host species is present, must be expected during the upcoming decades.

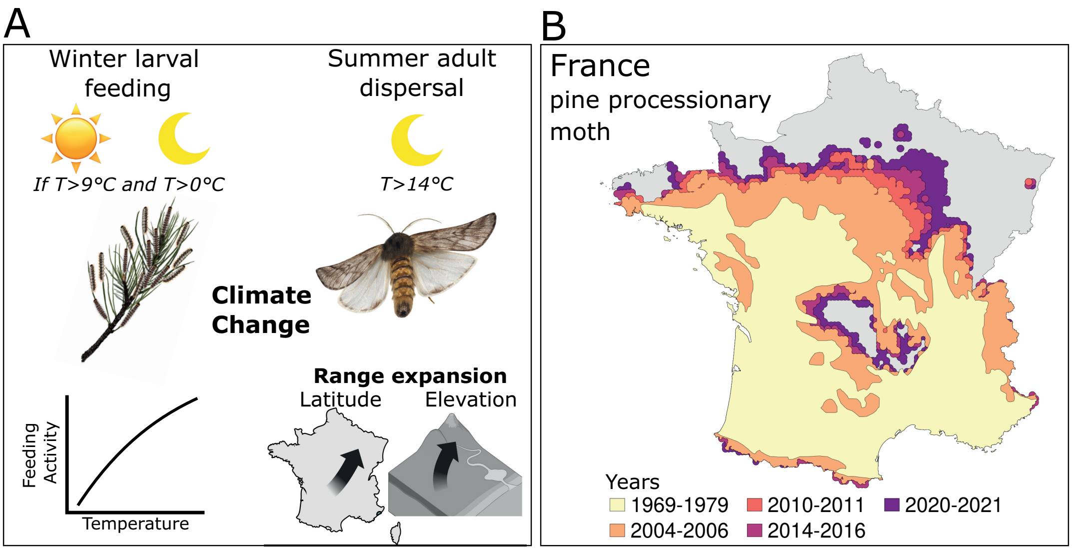

Fig. 4: Expansion of the pine processionary moth. A) Mechanisms driving the range expansion of the pine processionary moth, by increasing night temperatures that promotes feeding activity, larval survival during the winter and dispersal of female moths during the summer. Data from Battisti et al. 2005 and 2006, original drawings by Paolo Paolucci. B) Expansion of the pine processionary moth in France from 1969 to present (source J. Rousselet INRAE). The inlet for the range expansion was created with https://BioRender.com.

New threats from introduced pests and diseases

The oak lace bug spreading across Europe

The North-American oak lace bug (*Corythucha arcuata*) was first discovered in Northern Italy in 2000 (Bernardinelli & Zandigiacomo, 2000), has likely arrived with timber imports from the USA. Two years later, it was also found in Switzerland and Turkey and, after almost a decade of latency, it started to spread explosively, starting from Turkey through the Balkans (Csóka et al., 2020; Paulin et al., 2020). As a typical 'hitchhiker', it travels very fast by using rail and road transportation, and has now been recorded already in 27 European countries (Fig. 5), reaching Southern Poland at the northern edge of its current distribution. A recent study evaluated that practically all Eurasian deciduous oak species are suitable hosts, allowing the insect to spread potentially into more than 35 million hectares of oak forests in Europe alone (Csóka et al., 2020). The oak lace bug has a good cold tolerance during overwintering and develops two, sometimes up to three seasonal generations in Europe. Both nymphs and adults suck on the underside of the leaves and, at high abundance, the entire foliage may wilt. Ultimately, the canopy desiccates and leaves shed 1–2 months earlier than usual. Infestations by oak lace bugs reduce tree growth, vitality and fruiting and they have negative downstream impacts on the extremely rich food web (herbivore insects, mycorrhiza fungi etc.) in oak forests (Nikolić et al., 2019; Paulin et al., 2020). Repeated defoliations can lead to predisposition to further attack also by other insects or pathogens, which can ultimately lead to mortality years later (Hartmann & Messier, 2008). The insect has no native specialist antagonists, and generalist natural enemies, or entomopathogens native to Europe, have not yet shown any regulatory potential. In 2019, the estimated area of the severe infestation in Europe (including European parts of Russia) was approximately 1.75 million hectares, which has almost doubled since then. Given the large geographic distribution of oak species and anticipated further warming, the oak lace bug will very likely invade oak forests at large scale (Ciceu et al., 2024) with uncertain impacts on European oak forests.

I am working as a forest entomologist in Hungarian forests for almost 40 years now, and have been intrigued by oak forests and their pests in other continents like Asia and North America also. To me, the oak lace bug certainly is the most dangerous invading insect of all time in our oak forests, if not all European forests. The insect has very quickly and unexpectedly become a major factor in the "damage chain" of oak decline triggered by climate change. Due to its devastating effects on oak fecundity, I fear that it will severely hamper both natural and artificial oak regeneration. As a side effect, lace bug damage may also threaten the outstandingly high biodiversity in our oak forests and poses a serious risk to almost all valuable ecosystem services provided by them. I worry that these beautiful forests, our cultural heritage, and their astonishing diversity will change completely with ongoing climate change and biological invasions.

György Csóka, Hungary

Invasion of European chestnut forests by Dryocosmus kuriphilus

The process of invasion of European chestnut (*Castanea sativa*) forests by Dryocosmu *kuriphilus*, the Asian Chestnut gall wasp, is remarkable for two reasons. First, the speed with which it spread was impressive. Introduced from China with forest nursery material and first detected in Italy in 2002, the insect reached France in 2007, Germany in 2012, Portugal in 2014 and the UK in 2015 (Avtzis et al., 2019). After its arrival in France in 2007, it spread throughout almost all of the country's chestnut forests within 11 years only, at an expansion rate of around 100 km/year (Fig. 6; DSF data). This is even greater than early estimates of long dispersal distances from Italy (76 km/year; Gilioli et al., 2013), which can only be explained by human-assisted transport, in particular via transfer of contaminated plants, but also by its well-developed flight capacity, further supported by wind.

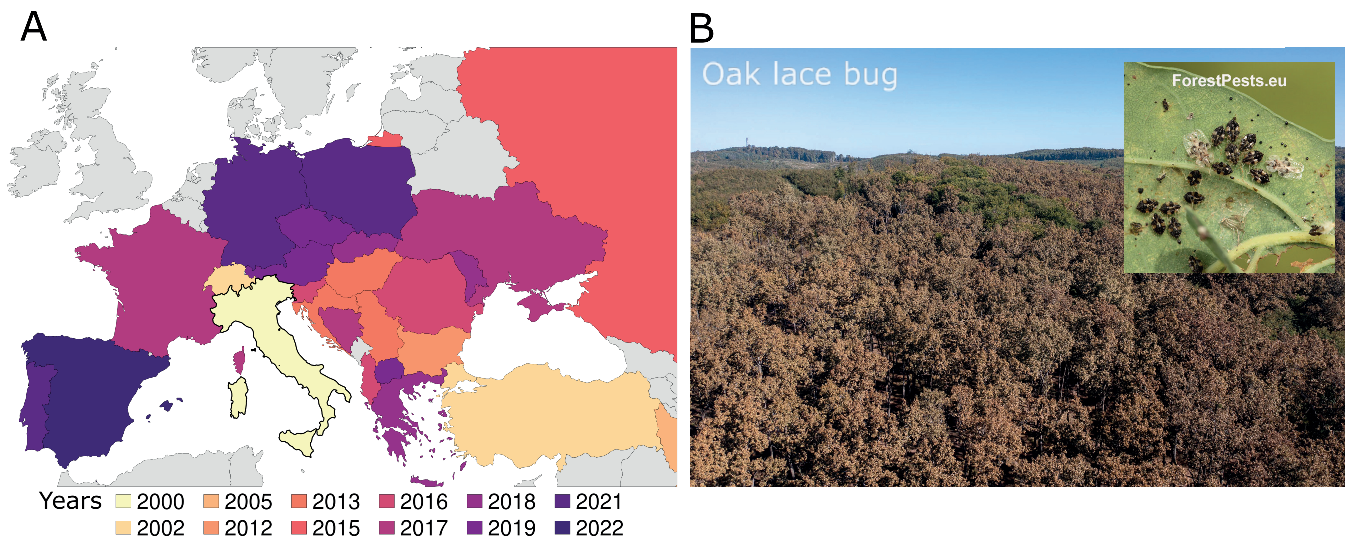

Fig. 5: Canopy wilting (B) caused by oak lace bug sucking on the bottom side of oak leaves (inlet) and progress of the oak lace bug invasion across Europe (A).

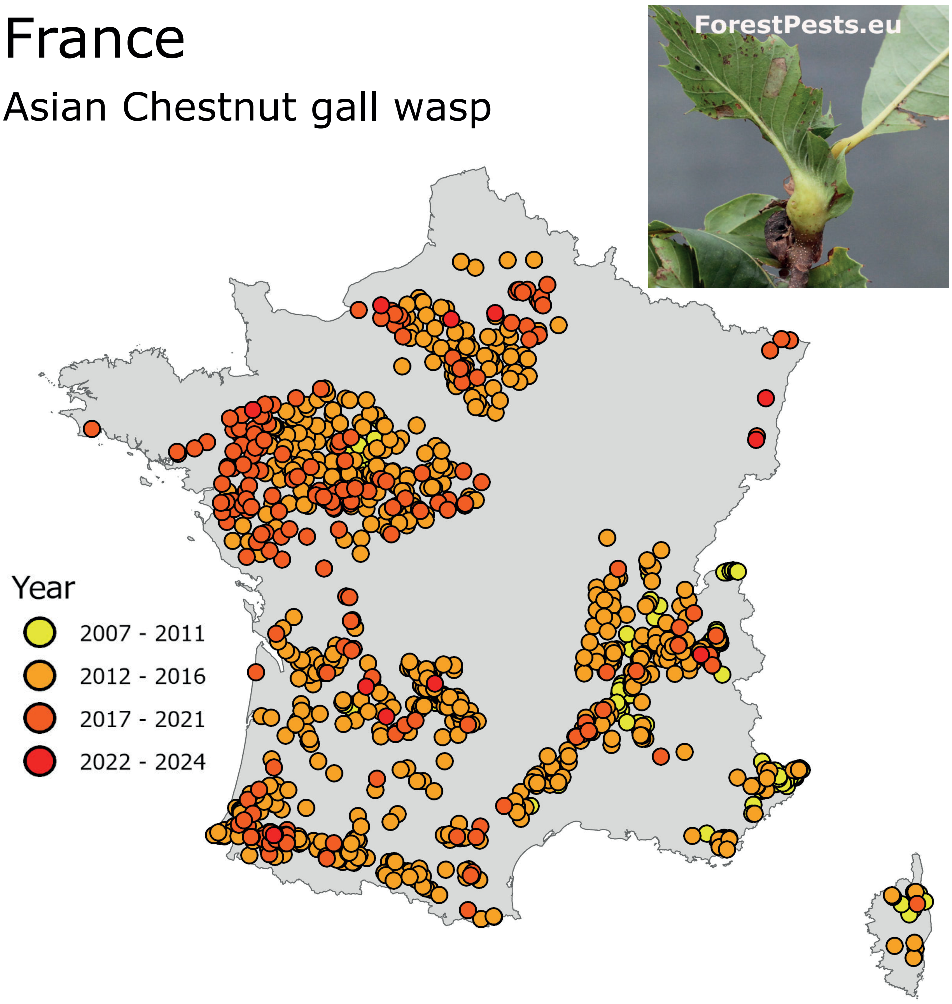

Fig. 6: Spread of the Asian Chestnut gall wasp in France since its arrival in 2007 and estimate of the spread rate (Data DSF, French Ministry of Agriculture). Inlet: ForestPests.eu, photo by M. Zúbrik.

The impact of this invasive insect was significant since it was first introduced, as the deformation of young twigs and leaves causes growth reduction in attacked trees and, above all, a decline in chestnut production of up to 80% in heavily attacked trees (Battisti et al., 2014).

I have been working in forest protection and entomology for more than 35 years and noticed how fast climate change affects our forests. If current climate trends continue, we can expect to see even more frequent and stronger storms, severe droughts and other climate extremes. I do not think we can stop climate change fast enough to protect our current forests, so our focus should shift towards identifying and promoting development of forests that are better adapted to new climates, like planting of tree species that are more suitable for future conditions. This may involve planting European tree species in new locations, but also non-native tree species. Conservation of current forests, without gradual, deliberate changes in tree composition, can have very negative long-term effects on the state of our European forests.

Milan Zúbrik, Slovak Republic

An introduced fungal pathogen causes ash dieback throughout Europe

European common ash (*Fraxinus excelsior* L.), an economically and ecologically important forest tree species, has shown first symptoms of ash dieback (ADB) in 1992 in northwestern Poland. The causal agent of ash dieback was first described as *Chalara fraxinea* in 2006 (Kowalski, 2006), and renamed in 2014 as *Hymenoscyphus fraxineus* ((T. Kowalski) Baral, Queloz & Hosoya). Most European common ash trees are highly susceptible to *H. fraxineus*, with only a minority (<5%) showing partial resistance or tolerance to acute dieback (McMullan et al., 2018). The pathogen has rapidly spread across the continent, causing significant mortality of ash trees in forests (Goberville et al., 2016) and often leads to mass dieback (Carroll & Boa, 2024). In Slovakia, the pathogen was first detected in 2004 (Kunca & Leontovyč, 2011) and the amount of salvaged ash timber increased 7-fold within the last 10 years (Fig. 7). Trees infested by *H. fraxineus* are often colonized and subsequently attacked by secondary pests such as ash bark beetles – *Hylesinus varius* and *Hylesinus crenatus* or fungal pathogens like *Armillaria* spp. (Kunca et al., 2019).

The emerald ash borer adds further pressure on ash in Europe

Ash forests not killed by *H. fraxineus* may become threatened by yet another invasive species, the emerald ash borer (EAB), *Agrilus planipennis* (Fairmaire, 1888). This phloem-boring beetle is native to East Asia (China, Japan, Taiwan, South Korea, etc.) where it is considered a minor pest, preferentially attacking weakened or dying ash trees (Baranchikov et al., 2008; Schans et al., 2020). The EAB has become one of the most serious invasive insect pests in North America since first time detected in 2002 (Baranchikov et al., 2008; Herms & McCullough,

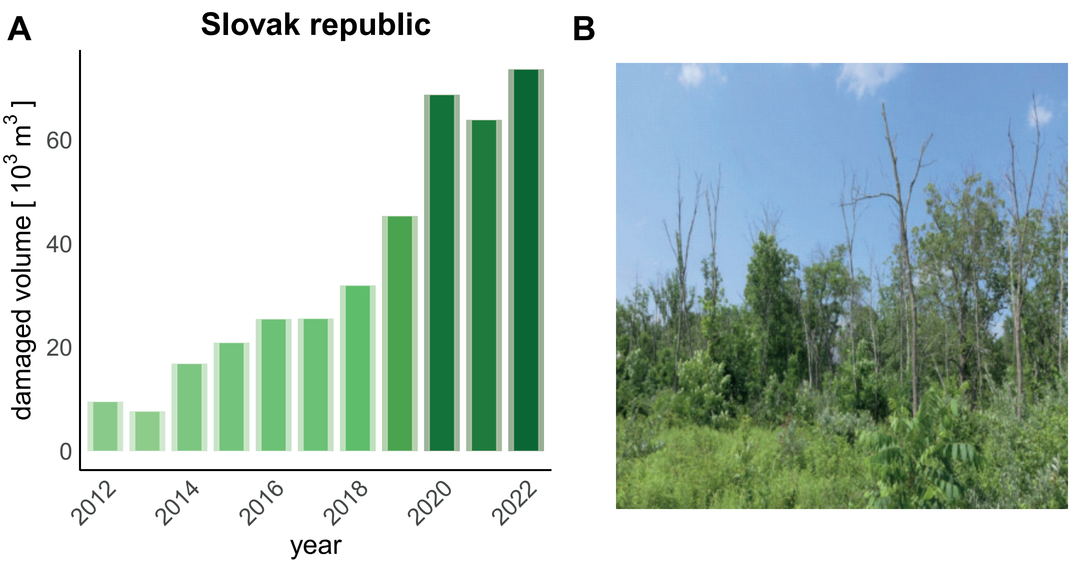

Fig. 7: Amount of annual salvaged ash timber in the Slovak republic from 2012 until 2022 in thousands of m^3. Data from official state statistical evidence. Right: Degradation and fast dieback – these are main characteristics of ash forest stands after attack by *A. planipennis* (Photo: G. Csoka).

2014). It has caused enormous economic losses in the USA and Canada, killing millions of ash trees (Poland et al., 2015). In Europe, the EAB has been first recorded in 2003 around Moscow, with a rapid rate of spread ever since (Selikhovkin et al., 2022). EAB was first detected in eastern Ukraine in 2019 where it has damaged both *F. excelsior*, and *F. pennsylvanica*, the affected area expanded from 13.3 hectares in 2019 to 1212 hectares by 2023 (Davydenko et al., 2022). Field surveys from 2019 to 2022 indicated that EAB is expanding further west quite rapidly. The beetle was commonly found on ash trees with visually healthy crowns, not exhibiting ash dieback symptoms indicating that EAB attacks and kills ash trees regardless of their health status (Davydenko et al., 2022). In Ukraine, the estimated yearly spread rate of EAB was up to 16.5 km from the advancing front (data for January 2022). However, more recent evidence showed EAB spreading more rapidly via "hitchhiking" on transport vehicles, with the beetle found in Kyiv parks in 2022, over 500 km from its continuous invasive populations in eastern Ukraine. Additionally, a large proportion of non-native planted ash, particularly *F. pennsylvanica* from North America, often planted in city streets and along roads contributes to the rapid spread of EAB, that has advanced by 120 km between 2021 and 2023 (Skrylnyk et al., 2023).

As a forest pathologist with two decades of experience in forest protection, I have witnessed numerous challenges that our forests face. The current phenomenon of the rapid spread of the emerald ash borer and the concurrent presence of the ash dieback pathogen in Europe represents one of the most alarming threats to our ash populations. Managing affected stands is extremely challenging, and without significant changes in the tree species composition, it is practically impossible to preserve forests on many locations. Traditional methods of forest protection are proving inadequate in the face of such aggressive invaders. We must prioritize the development and implementation of integrated pest management strategies that include biological control agents, genetic resistance, and improved monitoring techniques.

Kateryna Davydenko, Sweden

Changes in interactions of native pests and diseases with their hosts

The secondary oak splendour beetle is increasingly behaving like a primary pest in Germany

For hundreds of years, old growth oak forests are typical features in many regions of Germany. Originating often from medieval management forms like pasture-woodland or coppice, many of those oak forests are protected nowadays as unique habitats and biodiversity hotspots. However, for some years now, in many German regions these oak forests have started suffering increasingly severe damage from oak jewel beetles (in particular the oak splendour beetle, *Agrilus biguttatus*). The beetles are thermophilic and occur naturally in oak forests, they are known to dwell in big dying branches in crowns of old oaks. Being a secondary pest, oak splendour beetles colonize tree trunks only if trees are severely weakened or already declining, for example after abiotic stress events like prolonged periods of heat and drought, or flooding (Hartmann & Blank, 1992; Lobinger, 1998; Reed, 2017).

Without additional damaging factors, the above-mentioned stressors alone result only in a temporary vitality decline of oaks and trees commonly recover well within a few years. By contrast, the recurrent heat and drought in Germany between 2018 and 2022 has weakened old oak stands to such an extent that even tree stems of previously vital trees were heavily colonized by jewel beetles. Ideal conditions for development of beetle broods led to massive exponential beetle population built-up since 2019, causing large-scale oak forest damage in some of the regions (NW-FVA, 2023).

The landscapes of my childhood in Northwest German lowlands were characterized by old, gnarled giant oaks (*Quercus robur*) growing in forests, but also along small and large country roads. Fields were separated by so-called "Knicks", hedges of wild vegetation crowned by old oaks. The region is characterized by Atlantic climate with temperate summers and relatively abundant precipitation, but climate change has brought us extreme summers there, too. The oak jewel beetle (*Agrilus biguttatus*) has not been able to spread into the lowlands yet, and many of the old oak structures are still preserved. However, I fear that with ongoing climate change even this region will be increasingly affected by pests such as the oak jewel beetle. This would entail an enormous ecological and economic damage, and would bring about a terrible loss of my cultural identity.

Rainer Hurling, Germany

Population growth of the oak jewel beetle can be actively controlled by sanitary cuts that remove attacked trees during an early stage of infestation (Lobinger et al., 2024). This reduces the number of developing beetles in the forest, and thus decreases growth rates of the daughter population. In the best-case scenario, timely sanitary cuts can even eliminate a beetle population. However, at current levels and speed of beetle infestation, forest owners are barely able to prepare and implement sanitary cuts ahead of further expansion. In many stands, the damage caused by oak jewel beetles therefore continues to grow uncontrollably. The extent of the current damage has not been observed before, particularly not in old-growth forests, which previously formed vital, large and closed forests. It is very likely that current developments in oak forests are linked to climate change (Sallé et al., 2014) and we must assume that such damage dynamics will occur even more frequently with further warming. Because oak trees require several years to recover from a beetle infestation, the time window between attacks may become too short for trees to regain vitality in the worst-case scenario. This then leads to a permanent predisposition making infestations of other pathogens very likely and questions the role of oaks as a promising species for shaping climate resilient forests in Germany.

Secondary bark beetle species become primary damage agents in pine stands

Bark beetle species have traditionally been categorized according to life-history traits and strategies into primary and secondary, aggressive and non-aggressive beetles (Six & Wingfield, 2011). While primary aggressive beetles can attack and kill vital trees, secondary non-aggressive beetles attack weakened trees that are already declining and contribute to accelerating the decline. However, climate change and anthropogenic pressure have shifted these ecological roles, where formerly considered non-aggressive bark beetles suddenly become aggressive (Six, 2020) and may now cause massive outbreaks and large-scale dieback of healthy trees.

Bark beetles are closely associated with ophiostomatoid fungi, also known as sapstain or blue-stain fungi, because they cause discoloration in phloem and sapwood (Jankowiak et al., 2017). Many bark beetle species symbiotically live with a variety of fungal associates that can detoxify tree defense compounds and serve as a food source for beetles (Zhao et al., 2019). Fungal presence during tree colonization by bark beetles is associated with reduced tree growth, crown thinning, needle chlorosis, and even tree death (Colombari et al., 2011; Davydenko et al., 2021; Davydenko et al., 2017; Villari et al., 2012). Aggressive ophiostomatoid fungi like *O. minus*, *Leptographium* sp., and *Graphium* sp. have shown to be among the most virulent pathogens to conifers in Europe (Davydenko et al., 2021). Along with the transition of bark beetles from secondary to primary damage agents, ophiostomatoid fungi associated with bark beetles now pose an additional and significant threat to forest health.

Two species of bark beetles, the pine engraver beetle (*Ips acuminatus*) and the six-toothed bark beetle (*Ips sexdentatus*), have become the most destructive pests in *P. sylvestris* forests within a couple of decades. Before the 2010s, these two species were considered to be of minor significance; not leading to outbreaks over large regions, however, recently they were reported as regularly causing extensive damage in young plantations and mature stands of *P. sylvestris* (Davydenko et al., 2021; Davydenko et al., 2017; Levieux et al., 1989; Siitonen, 2014). The species has transitioned from a formerly secondary insect to an aggressive primary damage agent that attacks and kills healthy trees across many countries such as Finland, Italy, Poland, Spain, Germany, Slovakia, and Ukraine (Bueno et al., 2010; Colombari et al., 2011; Davydenko et al., 2021; Dobor et al., 2020; Jankowiak et al., 2017; Siitonen, 2014). Drought-induced weakening of *P. sylvestris* trees and ensuing infestation by *I. acuminatus* and *I. sexdentatus* resulted in rapid tree dieback in Ukraine, causing the loss of about 70,000 hectares of plantation forests and leading to considerable economic loss (Davydenko et al., 2021).

Increased damage caused by Scots pine blister rust in Scandinavia

The rust fungus *Cronartium pini* causes Scots pine blister rust (SPBR) in Scots pine (*Pinus sylvestris*) and is a good example of a fungal pathogen that became a major issue in forest ecosystems where it was not before. In the early 1900s, only moderate blister rust damages were observed in Scots pine stands in northern Sweden and Norway (Jørstad, 1925; Lagerberg, 1912; Rennerfelt, 1947), but in recent decades heavily infected stands have been reported in Scandinavia and in Finland (Kaitera et al., 1994). During the last decades, SPBR epidemics have been causing severe damage in northern Sweden, increasing the public awareness of their relevance as a major forest threat. The Swedish National Forest Inventory included SPBR in their targeted forest damage inventory (TFDI) in 2008, 2012, and 2022 (Wulff & Hansson, 2009; Wulff & Hansson, 2013; Wulff et al., 2022). The results show that today, more than 130 000 hectares of pine forests are heavily infected and pine regeneration is severely threatened (Wulff & Hansson, 2009). At the time of writing, SPBR is considered one of the most severe forest diseases and causes the greatest economic loss for forest owners in Sweden (Skogsstyrelsen, 2017).

Samils & Stenlid (2022) suggested changes in precipitation regimes as one of the potential reasons for the increase in SPBR epidemics. The ongoing climate change is expected to shift the current disease situations, depending on the region (Dudney et al., 2021; Kovalenko et al., 2024). When comparing weather data from 1961 to 1990 and 1991 to 2018, precipitation during June, July and August has generally increased throughout Sweden (SMHI, 2023). During these three months, the aeciospores, urediniospores, and basidiospores of *C. pini* are released to infect either pine or alternate hosts. Therefore, increasing precipitation may have created optimal conditions for *C. pini* infection. Proportionally greater warming at higher latitudes will have greater ecological consequences (Post et al., 2019) and, for Sweden, this may induce a greater increase of SPBR incidence in the northern parts by the end of this century.

Increasing pressure from abiotic threats

Climate Change and the Escalating Intensity of Storm Events

Recent decades have seen a notable increase in both intensity and frequency of storm events globally, a phenomenon that closely aligns with changes in the climate system (IPCC, 2023). These alterations are primarily attributed to global warming, which has increased atmospheric moisture content and altered energy dynamics, leading to more intense rainfall and stronger wind events (Hoegh-Guldberg et al., 2022; IPCC 2023). There is evidence for a poleward shift in storm tracks, potentially increasing the frequency of extreme weather events in mid-latitude regions previously less affected (IPCC, 2007). This shift is also associated with higher cyclone activity across both hemispheres, again resulting in increased storm intensity in certain regions (Daloz & Camargo, 2018).

Ever since I was a child, I have been fascinated by atmospheric phenomena and their destructive power. Above all and most interesting to me were, and still are, storms. During the last decade, these powerful forces of nature have rapidly and unpredictably become significant contributors to environmental degradation, damaging ecosystems and human communities alike. Their destructive power can devastate natural habitats, threaten the provision of essential ecosystem services, and damage the infrastructure and landscapes, almost by a blink of the eye. Storms often leave behind ecosystems that hardly recover and are difficult to restore, and this makes me deeply concerned that our rich and diverse natural forest landscapes, and our cultural heritage, will undergo irreversible changes from such extreme weather events.

Marta Bełka, Poland

Derechos are meteorological phenomena characterized by swift-moving bands of thunderstorms that can cause large-scale wind damage, but are still rare (Johns & Hirt, 1987). With global warming, the conditions required for derecho formation, such as extensive, horizontally organized convective systems, are becoming more prevalent (Pendergrass, 2020), suggesting a greater potential for their occurrence under appropriate meteorological conditions.

An impressive derecho event occurred in Poland on the night of 11–12 August 2017, and it was among the most powerful storm incidents recorded in the region. This storm traveled from the Coast to Lower Silesia, over 300 km, and produced hurricane-force winds with speeds reaching up to 150 km/h (Chmielewski et al., 2020). The mesoscale convective system that developed during that night met the criteria for a derecho, marking it as an unusually intense incident not only in Poland, but also in comparison with similar events across Europe and the United States (Taszarek & Ziemiański, 2022).

The devastation caused by the derecho was staggering, with nearly 10 million cubic meters of trees uprooted and broken, and almost 120,000 hectares of forest damaged. In the Lipusz Forest District alone 2.3 million cubic meters of trees were killed (see: https://www.lasy.gov.pl/pl/informacje/aktualnosci/najwieksza-taka-kleska-w-historii-polskich-lasow). This event had profound ecological impacts, including significant damage of nature conservation assets, including 22 nature reserves, 15 bird protection areas, and 134 nature heritage habitat types (Natura 2000 network) managed by the Polish State Forests. The economic implications were also considerable, with total damages close to an estimated 250 million EUR and extensive impacts on forest management and the lumber industries. This event underscores the vulnerability of forest ecosystems to novel extreme weather, highlighting the necessity of adaptive management strategies to enhance resilience, by diversifying forest structure and landscape-scale forest planning.

The impact of wildfires in Mediterranean regions

Wildfires have historically driven forest dynamics in Mediterranean regions, which are characterized by high temperatures and low relative humidity during the summer that lead to a high load of easily inflammable fine fuel. Human activities have profoundly altered the fire regime by causing frequent ignitions, but also by fire fighting and modifications of fuel quantity and distribution. The anthropogenic factors have created a new complex fire regime out of natural equilibrium, that responds to both natural processes and changes in land use (Lloret & Zedler, 2009).

Climate change dramatically alters wildfire regimes by increasing the frequency of extreme fire weather conditions, like intense heat waves with very low air humidity (Jain et al., 2022). High temperatures facilitate unprecedented fire behavior particularly in presence of fuel accumulation on recently abandoned agricultural or pastoral lands (Duane et al., 2021). The resulting extreme fires release huge amounts of energy that cause fires to spread quickly and to seed new fires over large distances. Mega-fires occur when thresholds of fire-promoting weather conditions and fuel accumulation are simultaneously exceeded (Pausas & Keeley, 2021) and models indicate increased climatic fire risks in the Mediterranean and even in northern European regions (Turco et al., 2018).

The increasingly drier climate exposes Mediterranean forests to the risk of transforming into non-forested ecosystems interspersed with aridity-adapted woodlands. The challenge for forest managers is now to ensure forest conversion to more climate resilient states, while preventing wildfires that lead to irreversible pathways towards non-forested landscapes. Forest resilience after fire depends on mechanisms such as resprouting or seedling establishment, which are threatened by intense and frequent fires (Lloret & Zedler, 2009), because they alter soil properties, consume organic matter and destroy soil structure, ultimately leading to long-term nutrient loss. More frequent extreme rainfalls, also a consequence of climate change, exacerbate soil erosion, particularly where vegetation cover has been lost during fires (Morán-Ordóñez et al., 2020). As a result, forest resilience is hampered by the interplay of increasing aridity and changing wildfire seasonality, recurrence, and severity (Fig. 8, Baudena et al., 2020; Díaz-Delgado et al., 2002).

Crucially important for the resilience of Mediterranean forests, i.e. their capacity to remain forests after fire, is whether future wildfire regimes will push them beyond a tipping point towards non-forested ecosystems. The Mediterranean region may provide a glimpse of what many European forests will be facing in an increasingly hotter and drier world. Forest managers must now implement adaptive strategies to strengthen forest resilience in the face of compound threats from wildfires, droughts, and pest outbreaks even in more northern regions that are currently still relatively moist and cold.

In the summer of 1994, a wave of wildfires hit Spain and the impact on public awareness was enormous, putting pressure on the scientific community to address this issue. Together with Josep Piñol, who is a modeler of fire behavior, I decided to analyze the number of climatic high-risk days throughout the 20th century and to relate them with burned area. Our study showed that, back in 1998 already, climate change was increasing wildfire risks. Since then, this evidence has been consolidated and models predict that this risk will further increase. This new wildfire regime also entails explosive fires, exacerbated by larger fuel loads from more arid climate. We now feel very close to the point when forest resilience will be overwhelmed and new landscapes will emerge.

Francisco Lloret, Spain

Outlook

In the preceding chapters, we have documented new threats to the health and persistence of European forests, as we know them today. Extreme droughts and high temperatures, large outbreaks of bark beetles and other tree-feeding insects, and non-native invasive pathogens that kill trees have combined to cause levels of damage unprecedented in the documented history of Europe's forests. These events are not happening in isolation, and many involve multifactorial interactions between abiotic and biotic factors. For example, increased temperatures and droughts stress trees and weaken their defenses against insects and pathogens, while at the same time, higher temperatures increase the number of generations and therefore the reproductive rate of some insects (such as the spruce bark beetle). The combination of stressed susceptible trees and insect outbreaks has been happening across much of Europe, and this is likely to become a new normal. Globalised international trade, the other main driver of the large-scale decline in forest health, has led to the arrival and establishment of numerous pathogens and insects which damage or kill trees. Some of these non-native organisms also benefit from the new and now more favourable climate and increased availability of susceptible trees, although others (such as ash dieback, dothistroma, and powdery mildews, which require cooler and more humid conditions) are expected to become less virulent in a warmer and drier climate. We can expect that these effects and their impacts on forests will worsen in the future, resulting in more extreme damage to Europe's forests. Interactions between native damaging insects and diseases will continue to be modified and shaped by ongoing warming and more frequent climate extremes as triggering events of forest decline form biotic factors. Some of the forest insects that are now considered secondary pests will become primary and tree killing insects, because climate warming creates conditions that are more favorable for insect population growth. At the same time, tree vitality will decline in regions with strong warming and increasing frequency of drought or heat events. Forest policy makers and forest managers will be struggling with unprecedented new situations, and will have to respond with utmost care

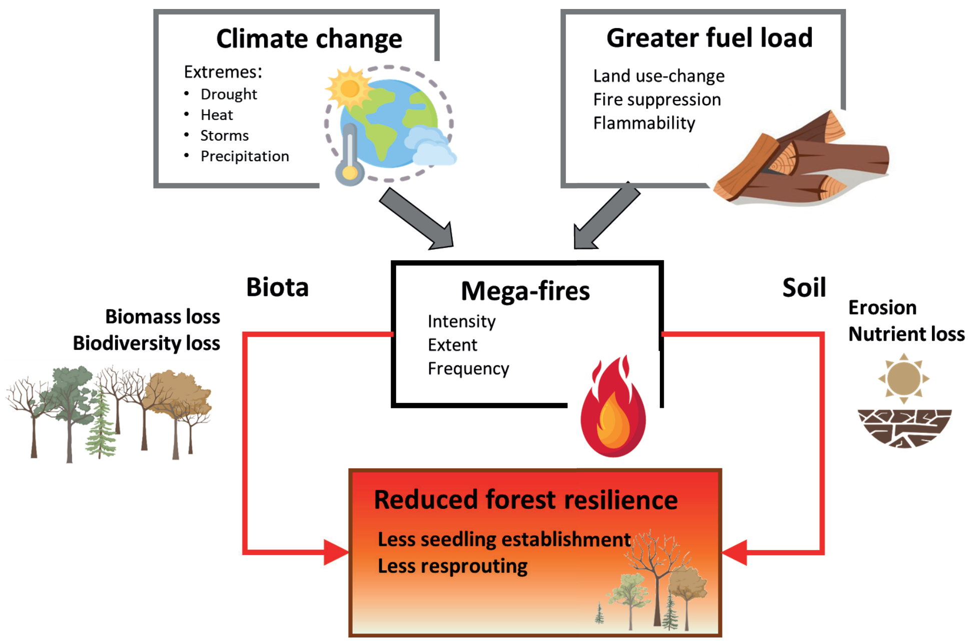

Fig. 8: Climatic change causes, via drought, heat and changing precipitation patterns or amounts, more appropriate conditions for fire ignition, and increases in fuel load and flammability. This can lead to mega-wildfires that have severe effects on vegetation via loss of biomass and biodiversity, and on soils by increasing erosion of denuded ground and loss of nutrients. These impacts together can severely reduce forest resilience and have the potential to cause shifts in vegetation types towards open forests or grasslands. Some of the elements have been created with https://BioRender.com.

and adaptability, embracing the unavoidable uncertainty of future climates.

New threats from introduced or invading damaging insects or diseases should be taken as potentially avoidable hazards, and treated as such. Measures to prevent importing such new threats are reinforced by governmental regulations, however, not always successfully as some of the examples presented in the sections above. There are several new threats to European forests, many of them mentioned in the EU Commission Delegated Regulation (EU) 2019/1702, and classified as "priority pests". Some of these pests have not yet been detected in the EU, others have been recorded recently, some even effectively eradicated. Among the dangerous pests for forests are: *Agrilus anxius*, a wood-boring beetle that can cause mortality in birch; *Aromia bungii*, an Asian longhorn beetle that devalues wood and can kill host trees mainly of the *Prunus* genus; *Bursaphelenchus xylophilus, an invasive nematode that causes lethal pine wilt disease*; or *Xylella fastidiosa*, an aerobic bacterial pathogen that develops in the xylem of many plant species and can cause sudden decline and dieback. These are just a few examples, many other species may enter the EU region via anthropogenic transport routes and cause devastating ecosystem damage of economical loss.

An example for a successful biological control measure against an invading insect is the invasion by the chestnut gall wasp. The wasp *Torymus sinensis* was selected as a parasitoid antagonist because of its high degree of specialization on *D. kuriphilus* and the synchronization of their cycles. It was successfully introduced in Italy and France at the end of 2000, barely 4 years after the arrival of the chestnut gall wasp. It soon became apparent that the parasitoid's dispersal speed was slower than that of its host (Avtzis et al., 2019), but this shortcoming was remedied by mass production and release. It took around 10 years after the start of biological control for chestnut groves to regain their initial vitality (Borowiec et al., 2018). From intensive observations and research it became apparent that mixed chestnut forests are more resistant to attacks by the gall wasps than pure forests, in particular because of the greater abundance of generalist parasitoids that develop on oak galls and are able to shift on the new host (Guyot et al., 2015). Such insights are important for shaping management strategies for resilient forests.

Some of the decisions taken today by policy makers or forest managers may prove successful in decades for maintaining functional forests for future generations, but it is unlikely that forests will look similar to the ones we appreciate now. In other circumstances, adaptive management attempts may fail, at least from the utilitarian perspective. Current host tree-insect/pathogen systems will evolve new dynamics, which we cannot anticipate with certainty, and these new dynamics may entail that some of the dominant forest tree species will recede and become minor components of future forests. However, forests will continue to exist in Europe, they are dynamic systems that have to rearrange themselves when the environment surrounding them changes. Forest management can help facilitate this transition by allowing new tree species to establish in locations where current forest composition dissolves and permanent forest cover loss is likely. Diversifying forest structure and landscape-scale forest management planning may improve habitat availability of antagonists and reduce the speed of spread of pests and diseases. For such decisions to be sustainable, they must be negotiated in an open societal dialogue, with the best available guidance by forest scientists.

Conflicts of interest

The author(s) declare that they do not have any conflicts of interest.

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