Climate drivers of bark beetle outbreak dynamics in Norway spruce forests

Lorenzo Marini[1,2], Bjørn Økland[3], Anna Maria Jönsson[4], Barbara Bentz[5], Allan Carroll[6], Beat Forster[7], Jean-Claude Grégoire[8], Rainer Hurling[9], Louis Michel Nageleisen[10], Sigrid Netherer[11], Hans Peter Ravn[12], Aaron Weed[13], Martin Schroeder[2]

[1]DAFNAE-Entomology, University of Padova, viale dell'Università 16, 35020 Legnaro, Padova, Italy

[2]Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE-750 07, Uppsala, Sweden

[3]Norwegian Institute of Bioeconomy Research, Box 115, N-1431 Ås, Norway

[4]Department of Physical Geography and Ecosystem Science, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden

[5]USDA Forest Service, Rocky Mountain Research Station, Logan, Utah 84321, USA

[6]Department of Forest & Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, BC, V6T 1Z4, Canada

[7]Swiss Federal Research Institute WSL Zürcherstr. 111, CH-8903 Birmensdorf, Switzerland

[8]Biological Control and Spatial Ecology, Université Libre de Bruxelles, CP160/12, 50 av FD Roosevelt, 1050 Brussels, Belgium

[9]Department of Forest Protection, Section Beetles and Test Plant Protection, Northwest German Forest Research Institute (NW-FVA), Grätzelstr. 2, D-37079, Göttingen, Germany

[10]Ministère de l'Agriculture, de l'Alimentation et de la Forêt, Département Santé des Forêts, Champenoux, 54280 Seichamps, France

[11]Department of Forest and Soil Sciences, BOKU – University of Natural Resources and Life Sciences, Institute of Forest Entomology, Forest Pathology and Forest Protection, Hasenauerstraße 38, 1190 Wien, Austria

[12]Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, DK-1958 Frederiksberg C., Denmark

[13]National Park Service, Inventory and Monitoring Program, Fredericksburg, VA 22405, USA

Corresponding author: Lorenzo Marini, DAFNAE-Entomology, University of Padova, viale dell'Università 16, 35020 Legnaro, Padova, Italy. E-mail: lorenzo.marini@unipd.it. Tel.: +39 049 8272807

ABSTRACT

Bark beetles are among the most devastating biotic agents affecting forests globally and several species are expected to be favored by climate change. Given the potential interactions of insect outbreaks with other biotic and abiotic disturbances, and the potentially strong impact of changing disturbance regimes on forest resources, investigating climatic drivers of destructive bark beetle outbreaks is of paramount importance. We analyzed 17 time-series of the amount of wood damaged by *Ips typographus* (L.), the most destructive pest of Norway spruce forests, collected across 8 European countries in the last three decades. We aimed to quantify the relative importance of key climate drivers in explaining timber loss dynamics, also testing for possible synergistic effects. Local outbreaks shared the same drivers, including increasing summer rainfall deficit and warm temperatures. Large availability of storm-felled trees in the previous year was also strongly related to an increase in timber loss, likely by providing an alternative source of breeding material. We did not find any positive synergy among outbreak drivers. On the contrary, the occurrence of large storms reduced the positive effect of warming temperatures and rainfall deficit. The large surplus of breeding material likely boosted *I. typographus* population size above the density threshold required to colonize and kill healthy trees irrespective of other climate triggers. Importantly, we found strong negative density dependence in *I. typographus* that may provide a mechanism for population decline after population eruptions. Generality in the effects of complex climatic events across different geographical areas suggests that the large-scale drivers can be used as early warning indicators of increasing local outbreak probability.

INTRODUCTION

Climate is currently changing at an unprecedented rate with potentially profound effects on disturbance regimes in forest ecosystems (Ayres and Lombardero 2000; Weed et al. 2013). Bark beetles are amongst the most devastating biotic agents affecting forests globally (Anderegg et al. 2015) and several species are expected to be favored by climate change (Worrell 1983; Jönsson et al. 2009; Bentz et al. 2010). In particular, the combination of increasing frequency of drought events and warmer temperatures are considered important predisposing factors triggering bark beetle outbreaks directly by affecting insect population dynamics, and indirectly through alteration of host plant growth and defense (Jactel et al. 2012; Weed et al. 2013; Hart et al. 2013; Raffa et al. 2015; Bentz and Jönsson 2015; Meddens et al. 2015). Given the potential interactions of insect outbreaks with other biotic and abiotic disturbances and the potentially strong impact of changing disturbance regimes on forest resources (Buma 2015), investigating the climate drivers of bark beetle outbreaks is of paramount importance.

In Europe, *Ips typographus* (L.) is considered one of the most destructive pests of conifer forests causing significant economic losses on a regular basis (Grégoire et al. 2015). At low population densities, *I. typographus* breeds in fresh wind-thrown or dying spruces and usually does not succeed in colonizing healthy trees that are protected by effective defense mechanisms (Krokene 2015). Extensive drought or windfall events can trigger beetle outbreaks by lowering tree resistance or raising the population size above the density threshold required to colonize and kill healthy trees (Christiansen and Bakke 1988). Such outbreaks may last several years, can cause important economic losses (Schelhaas et al. 2003), and usually end when the supply of suitable breeding material is exhausted or trees recover their resistance (Økland and Bjørnstad 2006).

At the regional scale, *I. typographus* population dynamics is expected to be strongly affected by climatic factors (Kausrud et al. 2011). Warmer spring and summer temperatures generally accelerate bark beetle development, thus increasing attack probabilities for standing forests (Jönsson et al. 2009; Marini et al. 2012). Moreover, severe drought events combined with warm temperatures can impair tree water supply and enhance tree susceptibility to *I. typographus* attacks (Wermelinger 2004; Netherer et al. 2015). Storm disturbance is another key driver of population outbreaks as shown by several studies analyzing long term regional fluctuations of bark beetle damage (Økland and Berryman 2004; Økland and Bjørnstad 2006; Marini et al. 2013). Storms provide a surplus of suitable host material in the form of wind-thrown trees devoid of vital defenses. Mass propagation of bark beetles even in small storm gaps potentially results in gradations strongly impacting the surrounding, still standing forests (Schroeder 2010; Kärvemo et al. 2014). Despite ample investigation of these factors regionally, a large-scale synthesis of outbreak data is still missing.

Potential positive synergies between density-independent processes such as climate drivers may also affect outbreak propensity. A positive synergy implies interactions among drivers whereby the total effect on a population outbreak is greater than the sum of each individual driver contribution. For instance, standing trees may be at higher risk of mortality when drought and high temperatures coincide (e.g. 'hotter drought' Millar & Stephenson 2015), or when the effects of storm and drought co-occur (Worrell 1983). In previous studies analyzing time-series of *I. typographus*-caused tree mortality (e.g. Økland and Berryman 2004; Marini et al. 2013), the low frequency of storms, the short length of the time-series and the relatively small spatial extent of the regions examined have constrained the exploration of these synergies. Although these interactions have often been hypothesized based on observations of single regional

outbreaks (reviewed in Wermelinger 2004; Kausrud et al. 2011) no large-scale
empirical test has been possible to date. This significant knowledge gap is currently
preventing our ability to predict the potential destructive impact of *I. typographus* under
a global change scenario.

Although the role of top-down biotic factors is considered secondary
compared to the abiotic triggers explained above (Marini et al. 2013), a strong
indication for a negative density feedback regulating *I. typographus* populations was
shown at the regional scale (Økland and Berryman 2004; Marini et al. 2012, 2013).
First, availability of breeding material can strongly regulate *I. typographus* populations
given, for instance, the lack of suitable stressed trees after large demographic
explosions. Second, at high population density when offspring are forced to attack
unsuitable healthy trees, many individuals are exposed to the risk of colonization failure
or at least of lower performance (Komonen et al. 2011). Understanding how density-
dependent factors affect attack dynamics may be critical for predicting the future
trajectory of outbreaks.

Distribution of *I. typographus* in Western Europe covers a wide climatic
range from Scandinavia to the Southern Alps. Despite proven local correlations
(reviewed in Wermelinger 2004; Kausrud et al. 2011; Grégoire et al. 2015; Seidl et al.
2015), it is unknown to what extent the drivers described above control outbreak
dynamics along this broad latitudinal gradient. Furthermore, potential synergies among
drivers have been largely overlooked, although we expect that several variables
associated with climate change may interact to influence outbreak dynamics. Here, we
examined 17 time-series collected across Europe documenting timber volume loss due
to *I. typographus*. When attacking standing trees, *I. typographus* is obliged to kill the
plant to reproduce. Hence, tree mortality is expected to be positively related to

population abundance. This is the largest such time-series analysis that we know of, describing volume of timber loss over the last three decades. Specifically, we aimed to quantify the relative importance of direct key climate drivers - i.e. temperature warming, rainfall deficit and storms - also testing for potential positive synergies among outbreak drivers.

MATERIALS AND METHODS

Study region

The study included 17 separate time-series, each from a different geographic area from 8 different European countries (Fig. 1). Each country developed their own monitoring program resulting in one or more time-series. The spatial distribution of the areas covered a wide latitudinal gradient capturing most of the climatic range of spruce including the southernmost (Italy) and the northernmost part (Scandinavia) of the species range (for a detailed description see Supplementary material Appendix 1). The 17 areas differed in territory size from a minimum of c. 10,000 to a maximum of c. 100,000 km^2. At this spatial resolution, we expected local variables such as topography and forest structure and management to be less important than climate drivers. Some areas comprised the natural range of spruce while others consisted solely of artificially planted forests (Table 1). Spruce growing stock varied significantly between areas and regional forest management ranged from selective cutting to clear-cut. As common practice in all areas, wind-thrown timber was salvaged, i.e. breeding substrates were preventively removed. Timely removal of wind-thrown timber is considered a key practice in the integrated management of *I. typographus* across Europe (Wermelinger 2004). However, a complete and timely removal of wind-thrown timber and standing infested trees was not always possible because single wind-felled trees, and small groups of killed trees are hard to detect and costly to remove. After extensive storm

events (e.g. storm 'Gudrun' in Sweden in 2005) large amounts of wind-thrown timber remained in the forest during the first summer due to limited harvesting resources. In addition, in strict reserves (e.g. National Parks in Germany or Austria) no harvesting is permitted. According to regional climate, univoltine populations (one generation per year) are predominant in the North and at high elevations in the Alps, while bivoltine populations (two generations per year) prevail towards the South and at lower elevations in Europe (Wermelinger 2004).

Data on timber loss

For each area, data were assembled from separate national forest monitoring programs. A single time-series was available for 5 countries (Sweden, Norway, Italy, Austria, and Belgium) while Switzerland, France, and Germany provided several time-series relating to specific sub-regions (Fig. 1). *Ips typographus* populations have a natural tendency to aggregate and produce easily recognizable groups of trees that are killed in any given year (hereafter labeled 'spots') (Marini et al. 2012). For each area, we built a time series of annual timber loss by summing the volume of standing trees killed (m^3) that occurred each year. Estimates of annual timber loss also included spots that were not detected until the following year. These data describe the delay between beetle attacks in late summer by second or even third generations, and the visible symptoms of tree death (discolored foliage) in the following spring (see Supplementary material Appendix 1 for more details about the methods). The basic assumption of our modeling approach is that the volume of timber loss was directly and monotonically related to *I. typographus* population density (e.g., Faccoli 2009; Kausrud et al. 2011). For a similarly aggressive bark beetle in the southern U.S., time series analyses of beetle population dynamics gave very similar results whether based on timber losses or insect abundance (Friedenberg et al. 2008).

The data also included the volume of timber felled by storms in both winter and summer (see Supplementary material Appendix 1). The storm-felled volumes were linked to the first summer they were available for *I. typographus* reproduction. Although the methods of data collection differed among and within countries, our mixed model approach accounted for these differences between areas by including an appropriate random structure (see Data analysis section).

Climate drivers

Temperature is the most important determinant of developmental time and voltinism of *I. typographus* (Annila 1969; Wermelinger and Seifert 1998; Jönsson et al. 2011). Warm spring and summer temperatures support an earlier completion of the first filial generation and the establishment of sister and successive generation broods (Wermelinger and Seifert 1998). For each year, we quantified a thermal sum between 1st May and 30th July (*Temperature*) with a temperature threshold of $+5°C$ (Netherer and Pennerstorfer 2001; Jönsson et al. 2009). *I. typographus* normally overwinters as adults, and complete development to the adult stage prior to winter is usually required for survival (Faccoli 2002). Since direct winter mortality is not commonly an important factor in population dynamics (Faccoli 2002; Koštál et al. 2011; Marini et al. 2013), we did not include any climatic metric related to winter temperatures. In preliminary analyses we tested the effect of minimum winter temperatures (averaged across December, January and February) and found no effect. Due to the large number of potential drivers and interactions, to reduce model complexity we omitted this variable from the models presented in the main text.

Severe rainfall deficit is suggested to be an important factor explaining *I. typographus* population density in southern Europe (Faccoli 2009; Marini et al. 2012). Recently, drought-induced alterations in tree attractiveness and resistance to *I.*

typographus were experimentally documented (Netherer et al. 2015). To test for the effects of spring and summer drought we quantified the cumulative rainfall between 1st March and 31th July. To avoid correlation with thermal sums, we did not use temperature-based drought indexes. In the current data set rainfall and summer temperature were only weakly negatively correlated across the selected study areas (r_s=-0.258). For each of the 17 areas, we computed the climatic parameters as described above using daily climatic data derived from the European gridded observational dataset (E-OBS, version 6) with a spatial resolution of 0.5 x 0.5 degrees covering the period 1980-2011 (Haylock et al. 2008). We chose to use these data to have comparable and representative climatic time series across the 17 areas. As explained below our statistical approach focused on explaining the temporal dynamics in timber loss using the inter-annual variation in climate. Hence, the spatial resolution and the absolute values of the climatic data did not affect our analyses.

Data analysis

Dynamics of timber loss

Our dependent variable was the rate of timber loss $R=$ ln(*Timber loss_t/Timber loss_{t-1}*), where *Timber loss_t* is the volume of timber loss due to *I. typographus* in a given year *t*. When *R* is positive the timber loss increases from year t-1 to year t, and when it is negative the timber loss decreases from year t-1 to year t. In some regions, several years had timber loss values of zero. This indicated either that the species reproduced only in fallen trees or that the volume of attacked standing forests was too low to be detected by foresters. From a population dynamics perspective a density of 0 cannot occur, we therefore excluded these years from the analyses. The final dataset included a total of 355 data points (yearly data) across the 17 areas. We used a discrete model of population dynamics as the baseline for developing and comparing competing models

for inter-annual variation in volume of timber loss due to *I. typographus* attacks (Marini

et al. 2012). First, we hypothesized that *R* would exhibit endogenous negative feedback

(density dependence). If negative, this feedback is expected to be related to intra-

specific competition for breeding substrate (Økland and Berryman 2004), or to a shift to

more well-defended standing trees, resulting in higher beetle mortality and reduced

beetle productivity (see Komonen et al. 2011). In preliminary analyses we also tested

the effect of delayed density dependence (i.e. *Timber loss$_{t-2}$* see Marini et al. 2012) and

always found a much better fit to the data with a 1-year lag. Therefore, we did not

consider *Timber loss$_{t-2}$* in the detailed model selection procedure presented here.

As density-independent, exogenous variables we considered three climatic

predictors: *Temperature*, *Storm*, and *Rain*. Rainfall and temperature are expected to

have both a direct and indirect effect on insect performance (Baier et al. 2007) and were

therefore tested both in the previous (*Rain$_{t-1}$* and *Temperature$_{t-1}$*) and current year (*Rain$_t$*

and *Temperature$_t$*). Volume of forest felled by storm was only included with one year

lag (*Storm$_{t-1}$*) because killing of standing trees generally starts in the second summer

after a storm. During the first summer insects attack storm-felled trees, the offspring

switch to standing trees the second summer (Schroeder 2001; Kärvemo et al. 2014).

Along with the main effects we considered two groups of interactions that were

ecologically plausible. The first group included interactions between storm-felled trees

and current climate, i.e. *Storm$_{t-1}$* x *Rain$_t$* and *Storm$_{t-1}$* x *Temperature$_t$*. Strong support for

these interactions in the analyses would indicate that the climatic conditions during the

current year would have a different effect on timber loss rate depending on the

availability of storm-felled trees in the previous year. The second included potential

interactions between temperature (*Temperature*) and rainfall (*Rain*) tested with no lag

(t) and 1-year lag (t-1). This interaction should capture potential synergistic effects of low rainfall and high temperatures (i.e. 'hotter drought').

Our analyses were based on an information theoretic approach to evaluate alternative competing models involving the density-dependent and independent variables to explain timber loss rate (R) (Burnham and Anderson 2002). We used linear mixed effect models to estimate model parameters. We included area (n=17) within country (n=8) as a random factor to account for differences between monitoring methodology and local conditions. We fitted a random intercept model. With our information-theoretic approach we compared the fit of all the possible candidate models nested within the following statistical model (global model):

$R \sim$ main effects (*Timber loss$_{t-1}$+ Temperature$_t$ + Temperature$_{t-1}$+ Rain$_t$ + Rain$_{t-1}$+ Storm$_{t-1}$*) + interactions (*Rain$_t$* x *Storm$_{t-1}$* + *Temperature$_t$* x *Storm$_{t-1}$* + *Temperature$_{t-1}$* x *Rain$_{t-1}$* + *Temperature$_{t-1}$* x *Rain$_t$* + *Temperature$_t$* x *Rain$_{t-1}$* + *Temperature$_t$* x *Rain$_t$*)

Each explanatory variable included in the analyses was standardized within each area to mean 0 and standard deviation 1 to make slopes comparable. This standardization is necessary to correctly interpret effect sizes when interactions are included (Gelman 2008).

The fit of each model in the set was then evaluated using second-order Akaike's information criterion corrected for small sample size (AICc). The best fit is indicated by the lowest AICc (AICcMIN). In a set of n models each model i can be ranked using its difference in AICc score with the best-fitting model ($\Delta AICc_i$ = AICci–AICcMIN). A model in a set can be considered plausible if its ΔAICc is below 7 (Burnham et al. 2011). We also computed the model weight (w_i) as the weight of evidence in favor of each model. The weight w_i represents the relative likelihood of a model and can be interpreted as the probability that model i is the best model, given the data and the set of

candidate models. When there were more than one plausible model selected, we calculated a model-averaged partial coefficient for each predictor. Parameter estimates obtained by model averaging are robust in the sense that they reduce model selection bias and account for model selection uncertainty (Johnson and Omland 2004). To further avoid the inclusion of uninformative parameters in our model selection, we reported the 95% confidence intervals (CIs) around model-averaged partial slope coefficients. The predictor effect is supported when the unconditional CIs did not include zero (Arnold 2010).

To evaluate the goodness-of-fit of our models we quantified the marginal R^2_{GLMM} (Nakagawa and Schielzeth 2013), that gauges the variance explained by the fixed effects as a proportion of the sum of all the variance components (i.e. total variation). The multi-model inference analyses and the R^2_{GLMM} estimation were performed using the 'MuMIn' package (Barton 2014) implemented in R version 2.13.0.

Before performing the multi-model inference analyses described above, we tested for potential collinearity between the predictors included in the global model using variation inflation factor (VIF). Usually a VIF>10 indicates severe multicollinearity problems (Neter et al. 1990). We fit the mixed model described above without interactions and computed the VIF for each predictor using the "car" package in R. All the predictors had a VIF<2 indicating very low collinearity in our dataset.

RESULTS

The multi-model inference analysis indicated that the rate of timber loss due to *I. typographus* was affected by several climatic variables with both additive and interactive effects. Overall, climate explained more than one third of the total variation across the 17 studied areas (Table 2). Model selection uncertainty was relatively low, and two models had $\Delta AICc_i$ <2 and 8 models had 2<$\Delta AICc_i$<7. The rate of timber loss

was related to summer temperatures and rainfall, i.e. the rate of timber loss due to *I.*
typographus increased after a dry year and when summer temperatures of the current
year were relatively high (Fig. 2). We found a positive effect of the volume of storm-
felled forests in the previous year on the rate of timber loss (Fig. 2). The variable *Storm*$_{t-1}$ (storm-felled trees) was log-transformed and therefore the response was strongly non-
linear. We also found strong support for a negative effect of the volume of timber loss
(i.e. trees killed by *I. typographus*) in the previous year (Fig. 2), suggesting negative
density-dependence in the *I. typographus* population. We did not find clear support for
the main effect of temperature in the previous year and rainfall in the current year on the
rate of timber loss. Because all the variables were standardized to mean 0 and SD 1, the
effect sizes indicated the relative importance of the climatic variables (Fig. 2). In all of
the plausible models ($\Delta AICc_i < 7$), three specific interactions were included. None of
them indicated a synergistic effect between drivers. The first was the interaction
between current year temperature and rainfall in the previous year suggesting that the
positive effects of warmer temperatures was unexpectedly reduced when rainfall in the
previous year was low (Fig. 3a). The second was the interaction between temperatures
in the current year and volume of storm felled trees in the previous year. This
interaction indicated that the effect of current temperatures on the rate of timber loss
was more pronounced when the previous year was characterized by relatively small
volume of storm-felled forests while the temperature effect diminished when the size of
the storms increased (Fig. 3b). The third was the interaction between rainfall in the
current year and volume of storm felled trees in the previous year; i.e. the negative
effect of current year rainfall on the rate of timber loss was more pronounced when the
previous year was characterized by small volume of storm-felled forests while this
effect diminished when the size of the storms increased (Fig. 3c).

DISCUSSION

Several climatic variables were important drivers of timber loss due to *I. typographus*, corroborating previous research showing that climate change can affect the outbreak dynamics of the most destructive pest of Norway spruce. Increasing summer temperatures, rainfall deficit and availability of storm-felled trees were strongly related to an increase in timber loss. Although we found no synergies between outbreak drivers, several interactions among drivers indicate that, even in the absence of storms, climate change stressors such as drought and temperature warming can boost bark beetle populations and increase forest damages. Our results suggest that the expected trends in climate change may have severe but predictable consequences for European spruce forests from the Alpine regions in the south to the Scandinavian regions in the north causing severe economic and ecological costs for European forests.

We found a strong positive effect of the volume of storm-felled forests in the previous year on the rate of timber loss due to *I. typographus*. After a wind-felling episode, large volumes of trees may be suitable for colonization and *I. typographus* populations can build up quickly (Christiansen and Bakke 1989; Stadelmann et al. 2014; Kärvemo et al. 2014; Grégoire et al. 2015). This fact underlines the urgent need for tools that allow for the reliable prediction of forest stand susceptibility to storm damage (Buma 2015), which will strongly improve our ability to predict *I. typographus* population dynamics (Seidl et al. 2011a). The effect was non-linear indicating a stronger effect on *I. typographus* attacks between years with no storms and years with moderate storms. This non-linear relationship could be explained by the fact that extremely large storms may create a surplus of wind-felled trees remaining in the forest that can be attacked by beetles also the second summer (at least under Scandinavian and Alpine climate conditions) (Schroeder 2010) thereby reducing the expected attacks on standing

trees again the second summer (Kärvemo et al. 2014). In addition, after extremely large storms the beetles may only be able to utilize a minor part of the storm-felled trees.

We found support for a positive effect of current summer temperatures on rate of timber loss due to *I. typographus*. Years with warm summers were generally characterized by an increase in timber loss. Warmer summer temperatures generally reduce bark beetle development time, increase performance and fitness, and are therefore expected to increase population impacts on forests (Bale et al. 2002; Jönsson et al. 2009; Stadelmann et al. 2013a; Bentz and Jönsson 2015). In our study the effect of warm temperatures was positive across South and North Europe, confirming the high plasticity of *I. typographus* in response to temperature variations (Dolězal and Sehnal 2007). The capacity of *I. typographus* to modify generation time with changes in thermal regimes allows the species to exploit improved thermal conditions both at low and high latitudes (Jönsson et al. 2009). In an earlier time-series study at the southernmost part of the host range, summer temperatures of the previous year emerged as a critical factor (Marini et al. 2012). This discrepancy was probably linked to local differences in population dynamics, i.e. in the south the effect of warm temperatures can contribute to impair host tree resistance more than in the regions investigated here.

In addition to the positive effect of current summer temperatures, low summer rainfall was an important driver of rate of timber loss. Several studies confirmed that lower than average summer rainfall seems to generally favor *I. typographus* infestations (Faccoli 2009; Marini et al. 2012, 2013). This is consistent with previous research indicating that drought may increase the availability of physiologically compromised trees and trigger *I. typographus* outbreaks (Kausrud et al. 2011). Recent experimental work has provided empirical evidence that water-limiting conditions impair Norway spruce resistance to bark beetle attacks (Netherer et al. 2015).

The response of spruce-bark beetle interactions to drought is therefore complex and more effort should be made to explore potential non-linear or interactive effects with other global change drivers (Lenton 2011; Meddens et al. 2015).

Contrary to general expectations, we found interactive but no synergistic effects of temperature warming, rainfall deficit and storms. The positive effect of temperature was more pronounced when other predisposing factors were absent, i.e. no large storms and no severe rainfall deficit. Insect population dynamics are expected to depend on both the availability of host material and the abiotic conditions for development and reproduction (Kausrud et al. 2011). After large storms the defense capacity of partially damaged, standing trees is likely reduced and thus a temperature or a rainfall effect on the beetles is less important because the insect populations may have surpassed thresholds that allow attack of healthy trees. Similarly to other bark beetle species, when this crucial population density is surpassed, positive feedback can predominate and factors that usually constrained low densities can be overcome (Raffa et al. 2008). The increase in timber loss was therefore less dependent on other abiotic factors when the storms were very large. There are several examples of large storms that were followed by large outbreaks, even if the year after the storm was not particularly dry or warm (e.g. Nikolov et al. 2015). Similarly, we found no effect of 'hotter drought' on *I. typographus* outbreak. Interestingly, the occurrence of a drought event in the previous year even tended to cancel out the positive effect of temperature warming.

We found a marked negative correlation between the rate of timber loss and the total volume of timber loss due to *I. typographus* in the previous year. This suggests that resource availability for breeding played a key role in regulating population sizes (Økland and Bjørnstad 2003; Økland and Berryman 2004). This relationship may be due to resource depletion, i.e. more attacks the year before consume

resources and make less susceptible host material available the following year. This natural mechanism of population regulation is likely associated with competition for breeding substrate, in addition to less favorable host quality (Økland and Berryman 2004; Marini et al. 2013). When local bark beetle populations become large compared to the availability of susceptible trees (i.e. storm-felled or standing stressed trees), colonization densities (i.e. number of maternal galleries per area) will be higher resulting in reduced reproductive success. In addition, insects may be forced to attack living and healthy trees resulting in higher attack density and lower reproductive success (Komonen et al. 2011). Defense capacity and relative resistance of healthy spruce trees are generally much larger than those of felled trees and may expose many individuals to the risk of colonization failure (Schiebe et al. 2012) or at least of a lower reproductive success (Komonen et al. 2011). The combination of host depletion and increased local competition may be responsible for the observed negative density-dependence (Kärvemo 2015).

The unexplained variation in timber loss dynamics was relatively high (ca. 65%), and a likely result of several factors. First, the direct influence of forest structure (e.g. age, growing stock etc.) and management is one putative driver for the observed variation in timber loss (Seidl et al. 2011b). However, due to the relatively large spatial extent of our study areas, we could not test ecologically meaningful forest variables. Second, although it has been considered that the role of top-down biotic factors is secondary compared to the abiotic triggers explained above, natural enemies can also drive *I. typographus* populations (Wermelinger 2004; Marini et al. 2012). Although natural enemies likely contributed to decreasing the frequency and/or extent of outbreaks, and could explain some of the variation in timber loss rate (Kausrud et al. 2011), the role of predation or parasitism in driving outbreak dynamics remains unclear.

CONCLUSIONS

Although the geographic areas investigated differed in outbreak magnitude, forest management, and general climate, we showed clear and predictable abiotic and biotic controls of *I. typographus* populations. Our results suggest that greater efforts should be made to integrate temperature warming, drought and storm effects into future scenarios of bark beetle outbreaks under global change (Seidl et al. 2009; Stadelmann et al. 2013a; Temperli et al. 2014) as their effects are not always additive. In particular the positive effect of warming temperatures was important only when no other abiotic triggers were present. These results are in contrast to expectations based on other bark beetles species showing that the compounded effects of several abiotic stressors should be larger than the contribution of the single one (Raffa et al. 2008; Millar and Stephenson 2015; Buma 2015). Moreover, increased competition for hosts after population eruptions can provide a natural mechanism for population decline (Marini et al. 2013), thereby increasing forest resilience at the regional scale. Despite this negative density-dependence, forest impacts during outbreaks can still be very large. Due to the central role of suitable breeding material in *I. typographus* population dynamics, it is crucial to implement long-term mitigation strategies to minimize availability of storm-felled and stressed standing spruce trees. Thus, more knowledge is needed about how different forest management methods affect spruce forest resistance to storms and subsequent bark beetle attacks (Stadelmann et al. 2013b; Temperli et al. 2014). A large proportion of variation in timber loss was dependent on variables that are beyond the influence of forest management (see also Seidl et al. 2015). Hence, finding generality in these complex climatic effects across different geographical areas is an important step in predicting forest disturbance regimes and understanding their ecological significance.

ACKNOWLEDGEMENTS

REFERENCES

Anderegg W. R. L. et al. 2015. Tree mortality from drought, insects, and their interactions in a changing climate. – New Phytol. 208: 674-683.

Annila E. 1969. Influence of temperature upon development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). – Ann. Zool. Fen. 6: 161-298.

Arnold T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. – J. Wildlife Manag. 74: 1175-1178.

Ayres M. P. and Lombardero M. J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. – Sci. Total Environ. 262: 263-286.

Baier P. et al. 2007. PHENIPS—a comprehensive phenology model of *Ips typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. – Forest Ecol. Manag. 249: 171-186.

Bale J. S. et al. 2002. Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. – Global Change Biol. 8: 1-16.

Barton K. 2014. MuMIn: Multi-Model Inference. R package version 1.12.1. http://CRAN.R-project.org/package=MuMIn

Bentz B. J. et al. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. – BioScience 60: 602-613.

Bentz B. J. and Jönsson A. M. 2015. Modeling bark beetle responses to climate change. – In Vega F. and Hofstetter R. (eds), Bark Beetles: Biology and Ecology of Native and Invasive Species, Elsevier Academic Press, San Diego, pp. 533-553.

Buma B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. – Ecosphere 6: 1-15.

Burnham K. P. and Anderson D. R. 2002. Model selection and inference: a practical information-theoretic approach. – Springer, Berlin

Burnham K. P. et al. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. – Behav. Ecol. Sociobiol. 65: 23-35.

Christiansen E. and Bakke A. 1988. The spruce bark beetle of Eurasia. – In Berryman A. A. (ed), Dynamics of Forest Insect Populations,. Plenum Publishing Corporation, New York & London, pp. 479-503.

Dolĕzal P. and Sehnal F. 2007. Effects of photoperiod and temperature on the development and diapause of the bark beetle *Ips typographus*. – J. Appl. Entomol. 131: 165-173.

Faccoli M. 2002. Winter mortality in sub-corticolous populations of *Ips typographus* (Coleoptera, Scolytidae) and its parasitoids in the south-eastern Alps. – J. Pest Sci. 75: 62-68.

Faccoli M. 2009. Effect of weather on *Ips typographus* (Coleoptera Curculionidae) phenology, voltinism, and associated spruce mortality in the Southeastern Alps. – Environ. Entomol. 38: 307-316.

Friedenberg N. A. et al. 2008. Temperature extremes, density dependence, and southern pine beetle (Coleoptera: Curculionidae) population dynamics in east Texas. – Environ. Entomol., 37, 650-659.

Gelman A. 2008. Scaling regression inputs by dividing by two standard deviations. – Stat. Med. 27: 2865-2873.

Grégoire J. - C. et al. 2015. Economics and politics of bark beetles. – In Vega F. and Hofstetter R. (eds.) Bark Beetles: Biology and Ecology of Native and Invasive Species, Elsevier Academic Press, San Diego, pp. 585-613

Hart S. J. et al. 2013. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. – Ecology 95: 930-939.

Haylock M. R. et al. 2008. A European daily high-resolution gridded dataset of surface temperature and precipitation. – J. Geophys. Res. 113: D20119.

Jactel H. et al. 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. – Global Change Biol. 18: 267-276.

Johnson J. B. & Omland K. S. 2004. Model selection in ecology and evolution. – Trends in Ecol. Evol. 19: 101-108.

Jönsson A. M. et al. 2009. Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, *Ips typographus*. – Global Change Biol. 15: 486-499.

Jönsson A. M. et al. 2011. Modelling the potential impact of global warming on *Ips typographus* voltinism and reproductive diapauses. – Climatic Change 109: 695-718.

Kärvemo S. et al. 2014. Dynamics of spruce bark beetle infestation spots: Importance of local population size and landscape characteristics after a storm disturbance. – For. Ecol. Manag. 334: 232-240.

Kärvemo S. 2015. Outbreak dynamics of the spruce bark beetle *Ips typographus* in time and space. Doctoral Thesis. Acta Universitatis Agriculturae Sueciae, 27.

Kausrud K. et al. 2011. Population dynamics in changing environments: the case of an eruptive forest pest species. – Biol. Rev. 87: 34-51.

Komonen A. et al. 2011. *Ips typographus* population development after a severe storm in a nature reserve in southern Sweden. – J. Appl. Entomol. 135: 132-141.

Koštál V. et al. 2011. Physiological and biochemical analysis of overwintering and cold tolerance in two central European populations of the spruce bark beetle, *Ips typographus*. – J. Insect Physiol. 57: 1136-1146.

Krokene P. 2015. Conifer defense and resistance to bark beetles. In Vega F.E. and
Hofstetter R. W. (eds) Biology and Ecology of Native and Invasive Species, Elsevier
Academic Press, San Diego, pp. 177-207.

Lenton T. M. 2011. Early warning of climate tipping points. – Nat. Climate Change 1:
201-209.

Marini L. et al. 2012. Climate affects severity and altitudinal distribution of outbreaks in
an eruptive bark beetle. – Climatic Change 115: 327-341.

Marini L. et al. 2013. Population dynamics of the spruce bark beetle: a long-term study.
– Oikos 122: 1768-1776.

Meddens A. J. H. et al. 2015. Patterns and causes of observed piñon pine mortality in
the southwestern United States. – New Phytol. 206: 91-97.

Millar C. I. and Stephenson N. L. 2015. Temperate forest health in an era of emerging
megadisturbance. – Science 349: 823-826.

Nakagawa S. and Schielzeth H. 2013. A general and simple method for obtaining R^2
from generalized linear mixed-effects models. – Met. Ecol. Evol. 4: 133-142.

Neter J. et al. 1990. Applied linear statistical models, 3rd edn. –Irwin, Chicago.

Netherer, S. and Pennerstorfer, S. 2001. Parameters relevant for modelling the potential
development of *Ips typographus* (Coleoptera: Scolytidae). – Int. Pest Manag. Rev. 6:
177-184.

Netherer S. et al. 2015. Do water-limiting conditions predispose Norway spruce to bark
beetle attack? – New Phytol. 205: 1128-1141.

Nikolov C. et al. 2015. Post-disaster forest management and bark beetle outbreak in
Tatra National Park, Slovakia. – Mt. Res. Dev. 34: 326-335.

Økland B. and Berryman A. 2004. Resource dynamics plays a key role in regional fluctuations of the spruce bark beetle *Ips typographus*. – Agric. For. Entomol. 6: 141-146.

Økland B. and Bjørnstad O. N. 2003. Synchrony and geographical variation of the spruce bark beetle (*Ips typographus*) during a non-epidemic period. – Popul. Ecol. 45: 213-219.

Økland B. and Bjørnstad O. N. 2006. A Resource-depletion model of forest insect outbreaks. – Ecology 87: 283-290.

R Development Core Team 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria ISBN 3-900051-07-0, URL http://wwwR-projectorg.

Raffa K. F. et al. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. – BioScience 58: 501-517.

Raffa K. F. et al. 2015. Natural history and ecology of bark beetles, In Vega F. E. and Hofstetter R. W. (eds) Biology and Ecology of Native and Invasive Species, Elsevier Academic Press, San Diego, pp. 1-40.

Schelhaas M. J. et al. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. – Global Change Biol. 9: 1620-1633.

Schiebe C. et al. 2012. Inducibility of chemical defenses in Norway spruce bark is correlated with unsuccessful mass attacks by the spruce bark beetle. – Oecologia 170: 183-198.

Schroeder M. 2001. Tree mortality by the bark beetle *Ips typographus* (L.) in storm-disturbed stands. – Int. Pest Manag. Rev. 6: 169-175.

Schroeder L. M. 2010. Colonization of storm gaps by the spruce bark beetle: Influence of gap and landscape characteristics. – Agric. For. Entomol. 12: 29-39.

Seidl R. et al. 2009. Modelling bark beetle disturbances in a large scale forest scenario model to assess climate change impacts and evaluate adaptive management strategies. – Reg. Environ. Change 9:101-119.

Seidl R. et al. 2011a. Climate change vulnerability of sustainable forest management in the Eastern Alps. – Climatic Change 106: 225-254.

Seidl R. et al. 2011b. Unraveling the drivers of intensifying forest disturbance regimes in Europe. – Global Change Biol. 17: 2842-2852.

Seidl R. et al. 2015. Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. – J. Appl. Ecol. 53: 530-540.

Stadelmann G. 2013a. A predictive framework to assess spatio-temporal variability by the European spruce bark beetle. – Ecography 36: 1208-1217.

Stadelmann G. et al. 2013b. Effects of salvage logging and sanitation felling on bark beetle (*Ips typographus* L.) infestations. – For. Ecol. Manag. 305: 273-281.

Stadelmann G. et al. 2014. Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. – For. Ecol. Manag. 318: 167-174.

Temperli C. et al. 2014. Cross-scale interactions among bark beetles, climate change and wind disturbances: a landscape modeling approach. – Ecol. Monogr. 83: 383-402.

Weed A. S. et al. 2013. Consequences of climate change for biotic disturbances in North American forests. – Ecol. Monogr. 83: 441-470.

Wermelinger B. 2004. Ecology and management of the spruce bark beetle, *Ips typographus* - a review of recent research. – For. Ecol. Manag. 202: 67-82.

Wermelinger B. and Seifert M. 1998. Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae). – J. Appl. Entomol. 122: 185-191.

Worrell R. 1983. Damage by the spruce bark beetle in south Norway 1970–80: a survey, and factors affecting its occurrence. – Medd. Nor. Inst. Skogforsk. 38: 1-34.

Supplementary material (Appendix A1 at <www.oikosoffice.lu.se/appendix>).

Appendix 1.

TABLE LEGENDS

Table 1 Main characteristics of the 17 areas included in the study.

Area	Size (km²)	Elevation range (m)	AMT in °C (reference elevation m a.s.l.)	Rainfall (mm)	Origin	Growing stock (m³ ha⁻¹)	Maximum size cut (ha)	Forest management	Number of generations	Mean *Ips* damage (m³ yr⁻¹)
S-South Sweden	87,712	0-300	5.0 (50 m)	620	Nat	173	20	Clear	1	149,605
N-SE Norway	96,877	0-1200	2.5 (700 m)	1250	Nat	165	5	Clear	1	210,716
D-Niedersachsen	47,614	0-600	8.7 (50 m)	785	Art	63	2	Shelter	2	53,557
D-Thüringen	16,202	100-1000	7.7 (350 m)	590	Art	151	2	Shelter	2	103,811
D-Rheinland-Pfalz	19,854	100-800	8.7 (300 m)	645	Art	78	2	Shelter	2	189,868
D-Baden Württemberg	35,751	100-1500	8.2 (500 m)	730	Art	151	2	Shelter	2	894,3069
D-Sachsen	18,420	100-1200	8.3 (300 m)	625	Art	139	2	Shelter	2	30,694
B-Wallonie	16,840	0-600	9.1 (150 m)	820	Art	338	5	Clear/Shelter	2-(3)	8,559
F-Alsace	8,280	100-1400	9.2 (350 m)	750	Nat	184	20	Clear/Selective	2	46,150
F-Lorraine	23,547	100-1400	9.3 (300 m)	890	Art	110	20	Clear/Selective	2	60,408
F-Champagne-Ardenne	25,606	100-600	10.0 (200 m)	738	Art	77	20	Clear/Selective	2	4,090
F-Franche-Comte	16,202	100-1400	8.9 (500 m)	1131	Nat	90	20	Clear/Selective	2	77,077
F-Rhône-Alpes	43,698	500-2000	8.5 (800 m)	1031	Nat	109	5	Clear/Selective	1-(2)	88,753
CH-Lowland	14,348	300-1200	8.9 (650 m)	1050	Art	390	1	Shelter/Selective	2-(3)	213,559
CH-Mountain	26,936	800-2000	5.3 (1400 m)	1350	Nat	350	1	Shelter/Selective	1-(2)	231,884
A-Austria	83,879	100-2000	6.4 (1000 m)	900	Nat/Art	175	2	Shelter/Selective	(1)-2-(3)	746,904
IT-Friuli Venezia-Giulia	7,844	100-2000	9.2 (600 m)	1110	Nat/Art	300	0.5	Selective	(1)-2-(3)	1,990

Abbreviations: Area: S (Sweden), N (Norway), D (Germany), B (Belgium), F (France), CH (Switzerland), A (Austria), IT (Italy); AMT: Annual mean temperature, Origin: Nat (natural spruce range), Art (outside natural spruce range); Forest management: Clear (clear-cutting of the whole stand followed by artificial plantations), Shelter (shelter-wood system where most of the trees are removed but regeneration is natural), selective (frequent selective cut of mature trees maintaining stand cover continuous).

Table 2 Results of the multi-model inference analysis testing the effects of climatic variables on the rate of timber loss across the 17 areas. For each model with ΔAICc<7, estimates are reported along with marginal R^2_{GLMM}, ΔAICc, and model weight (w_i). All variables were standardized to mean 0 and standard deviation 1. *Storm$_{t-1}$* was log-transformed before standardization.

Model rankuing	Intercept	$Temperature_{t-1}$	$Temperature_t$	$Storm_{t-1}$	$Timber\ loss_{t-1}$	$Rain_{t-1}$	$Rain_t$	$Temperature_{t-1} \times Rain_{t-1}$	$Temperature_{t-1} \times Rain_t$	$Temperature_t \times Storm_{t-1}$	$Temperature_t \times Rain_{t-1}$	$Rain_t \times Temperature_t$	$Storm_{t-1} \times Rain_t$	R^2_{GLMM}	ΔAICc	Model weight (w_i)
1st	-0.099		0.223	0.265	-0.351	-0.151	-0.052			-0.233	0.153		0.172	0.35	-	0.358
2nd	-0.094		0.237	0.262	-0.351	-0.149	-0.061			-0.231	0.160	0.032	0.180	0.35	1.56	0.164
3rd	-0.099	-0.006	0.224	0.265	-0.350	-0.152	-0.050			-0.234	0.155		0.172	0.35	2.14	0.123
4th	-0.114	-0.012	0.221	0.268	-0.352	-0.143	-0.055		0.073	-0.230	0.165		0.177	0.36	2.32	0.112
5th	-0.095	-0.006	0.238	0.262	-0.350	-0.149	-0.060			-0.231	0.162	0.032	0.180	0.35	3.71	0.056
6th	-0.096	0.009	0.215	0.266	-0.347	-0.154	-0.052	0.024		-0.233	0.158		0.171	0.35	3.95	0.050
7th	-0.110	-0.012	0.231	0.266	-0.352	-0.141	-0.061		0.068	-0.229	0.169	0.022	0.183	0.36	4.24	0.043
8th	-0.111	-0.001	0.215	0.269	-0.350	-0.144	-0.056	0.018	0.071	-0.230	0.166		0.177	0.36	4.30	0.042
9th	-0.092	0.008	0.230	0.263	-0.348	-0.151	-0.060	0.022		-0.231	0.164	0.030	0.179	0.36	5.60	0.022
10th	-0.107	-0.001	0.225	0.267	-0.350	-0.143	-0.061	0.017	0.066	-0.229	0.170	0.021	0.182	0.36	6.25	0.016

Fig. 1 a) Spatial location of the time-series and b) temporal fluctuations in timber loss due to *I.*

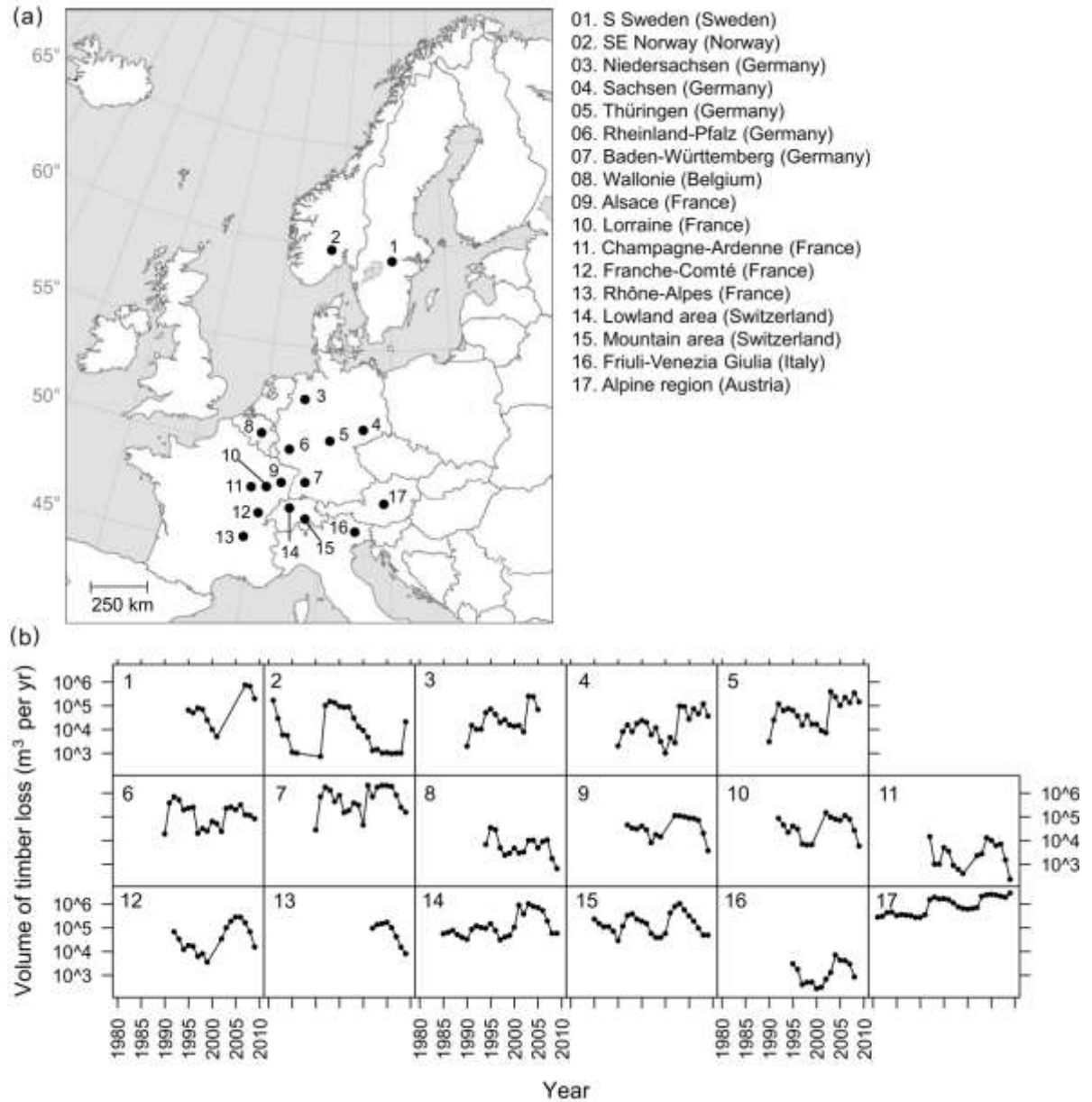*typographus* attacks to standing forests in the 17 study areas.

(a)

01. S Sweden (Sweden)
02. SE Norway (Norway)
03. Niedersachsen (Germany)
04. Sachsen (Germany)
05. Thüringen (Germany)
06. Rheinland-Pfalz (Germany)
07. Baden-Württemberg (Germany)
08. Wallonie (Belgium)
09. Alsace (France)
10. Lorraine (France)
11. Champagne-Ardenne (France)
12. Franche-Comté (France)
13. Rhône-Alpes (France)
14. Lowland area (Switzerland)
15. Mountain area (Switzerland)
16. Friuli-Venezia Giulia (Italy)
17. Alpine region (Austria)

Fig.2 Model estimates from the model-averaging procedure based on AICc information criterion. CIs indicate unconditional 95% confidence intervals for the variables included in the model set (all models included). Positive values are associated with an increase in *R* (timber loss rate). All variables were standardized to mean 0 and standard deviation 1 (i.e. effect sizes are comparable). *Storm$_{t-1}$* was log-transformed before standardization.
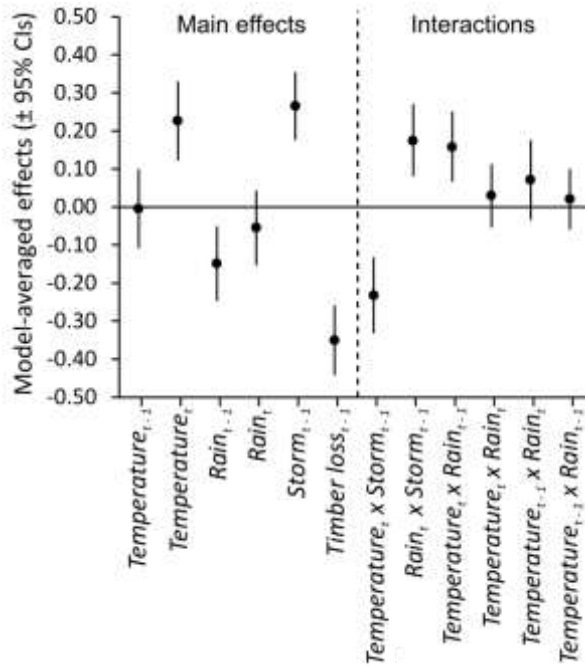
Fig. 3 The panels show the three interactions included in the set of plausible models: (a) *Temperature$_t$* x *Rain$_{t-1}$*, (b) *Temperature$_t$* x *Storm$_{t-1}$* and (c) *Rain$_t$* x *Storm$_{t-1}$*. R>0 indicates that the timber loss increased from year t-1 to year t. The plots were produced using the visreg() function in R in order to visualize the interaction between two continuous variables. The fitted lines indicate the model estimates while the shaded area indicated the intervals of confidence (95%). Cross-section between "low" and "high" was taken at the 50th quantile. For instance in (a) the observations were split according to rainfall: the observations on the left panel are below the median rainfall value while the observations on the right panel are above the median. All variables were standardized to mean 0 and standard deviation 1. *Storm$_{t-1}$* was log-transformed before standardization.