Forest disturbances under climate change

Rupert Seidl[1,*], Dominik Thom[1], Markus Kautz[2], Dario Martin-Benito[3,4], Mikko Peltoniemi[5], Giorgio Vacchiano[6], Jan Wild[7,8], Davide Ascoli[9], Michal Petr[10], Juha Honkaniemi[5], Manfred J. Lexer[1], Volodymyr Trotsiuk[11], Paola Mairota[12], Miroslav Svoboda[11], Marek Fabrika[13], Thomas A. Nagel[11,14], Christopher P. O. Reyer[15]

[1] Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences (BOKU) Vienna, Peter Jordan Straße 82, 1190 Wien, Austria

[2] Institute of Meteorology and Climate Research – Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology (KIT), Kreuzeckbahnstr. 19, 82467 Garmisch-Partenkirchen, Germany

[3] Forest Ecology, Department of Environmental Sciences, Swiss Federal Inst. of Technology, ETH Zurich, Universitätstrasse 16, CH-8092 Zürich, Switzerland

[4] INIA-CIFOR, Ctra. La Coruña km. 7.5, 28040 Madrid, Spain

[5] Natural Resources Institute Finland (Luke), Management and Production of Renewable Resources, Latokartanonkaari 9, 00790 Helsinki, Finland

[6] DISAFA, University of Torino, Largo Braccini 2, 10095 Grugliasco (TO), Italy

[7] Institute of Botany, The Czech Academy of Sciences, Zámek 1, CZ-252 43 Průhonice, Czech Republic

[8] Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, CZ-165 21 Prague 6 – Suchdol, Czech Republic

[9] Dipartimento di Agraria, University of Naples Federico II, via Università 100, 80055 Portici, Napoli, Italy

[10] Forest Research, Forestry Commission, Northern Research Station, EH25 9SY, Roslin, UK

[11] Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 129, Praha 6 Suchdol, 16521, Czech Republic

[12] Department of Agri-Environmental and Territorial Sciences, University of Bari "Aldo Moro", via Amendola 165/A, 70126, Bari, Italy

[13] Department of Forest Management and Geodesy, Technical University in Zvolen, T. G. Masaryka 24, Zvolen, 96053, Slovakia

[14] Department of forestry and renewable forest resources, Biotechnical Faculty, University of Ljubljana, Večna pot 83, Ljubljana 1000, Slovenia

[15] Potsdam-Institute for Climate Impact Research, P.O. Box 60 12 03, D-14412 Potsdam

* corresponding author: Email: rupert.seidl@boku.ac.at, Tel: +43-1-47654-91328

Key words: tree mortality; climate change impacts; abiotic disturbance; biotic disturbance; disturbance interaction; forest health

Around the globe forest disturbances are responding to ongoing changes in climate, increasingly challenging the sustainable provisioning of ecosystem services. Yet, our understanding of disturbance change remains fragmented, as disturbance processes are frequently studied independently and at local scales, disregarding interactions and large-scale patterns. Here we provide a comprehensive global synthesis of climate change effects on important abiotic (fire, drought, wind, snow & ice) and biotic (insects, pathogens) disturbance agents. Warmer and drier conditions particularly facilitate fire, drought, and insects, while warmer and wetter conditions increase disturbances from wind and pathogens. Widespread interactions between agents are likely to amplify disturbances, while indirect climate effects such as vegetation changes can dampen long-term climate sensitivities. Future disturbance change is likely to be most pronounced in coniferous forests and the boreal biome. The emerging disturbance trajectories call for a preparation of both ecosystems and society for an increasingly disturbed future of forests.

Natural disturbances such as fires, insect outbreaks or windthrows are an integral part of ecosystem dynamics in forests around the globe. They occur as relatively discrete events, and form characteristic regimes of typical disturbance frequencies, sizes, and severities over extended spatial and temporal scales [1,2]. Disturbances disrupt the structure, composition, and function of an ecosystem, community, or population, and change resource availability or the physical environment [3]. In doing so they create heterogeneity on the landscape [4], foster diversity across a wide range of guilds and species [5,6], and can initiate ecosystem renewal and reorganization [7,8].

Disturbance regimes have changed profoundly in many forest ecosystems in recent years, with climate being a prominent driver of disturbance change [9]. An increase in disturbance occurrence and severity has been documented over large parts of the globe, e.g., for fire [10,11], insect outbreaks [12,13], and drought [14,15]. Such alterations of disturbance regimes have the potential to strongly impact the ability of forests to provide ecosystem services to society [6]. Moreover, a climate-mediated increase in disturbances could exceed the ecological resilience of forests, resulting in lastingly altered ecosystems or shifts to non-forest ecosystems as tipping points are crossed [16–18]. Consequently, disturbance change is expected to be among the most profound impacts that climate change will have on forest ecosystems in the coming decades [19].

The ongoing changes in disturbance regimes in combination with their strong and lasting impacts on ecosystems have led to an intensification of disturbance research in recent years. There is a long tradition of disturbance research in ecology [3,20,21], with an increasing focus on understanding the links between disturbance and climate in recent decades [1,22,23]. Syntheses on the effects of climate change on important disturbance agents such as fire [24], bark beetles [25], pathogens [26], and drought [15] summarize recent advances of a highly prolific field of study. Considerably less synthetic knowledge is available on interactions among individual disturbance agents [27–29]. Furthermore, to date no global synthesis exists that integrates insights on changing disturbance regimes across agents and regions. Yet, the main drivers of disturbance change are global in scale (e.g., climate warming), rendering such a global synthesis highly relevant [30,31].

Specifically, a comprehensive analysis of the multiple pathways via which climate might influence forest disturbances is still lacking. Interactions between different disturbance agents can, for instance, result in strong and nonlinear effects of climate change on disturbance activity [32]. In contrast, climate-mediated vegetation changes can dampen the climate sensitivity of disturbances [33]. Many assessments of disturbance responses to climate change are currently neglecting such complex effect pathways [34,35]. More commonly still, the effects of changing disturbance regimes are disregarded entirely in analyses of future forest development [36,37] and studies quantifying the climate change mitigation potential of forest ecosystems [38], potentially inducing significant bias [39,40].

Here we review the current understanding of forest disturbances under climate change, focusing on naturally occurring agents of disturbance. Specifically, we synthesize the existing knowledge of how climate change may affect disturbance regimes via direct, indirect, and interaction effects. We reviewed the disturbance literature published after 1989, applying a consistent analysis framework over a diverse set of major forest disturbance agents, including four abiotic (i.e., fire, drought, wind, snow & ice) and two biotic agents (i.e., insects, pathogens). We compiled evidence for climate effects from all biomes and continents, and analyzed it in a qualitative modeling framework. We tested the hypothesis that climate change will considerably increase forest disturbance activity at the global scale, and specifically that positive, amplifying effects of climate change on disturbances dominate negative, dampening effects.

Literature review and analysis

We screened the literature for peer-reviewed English-language papers addressing the climate sensitivity of forest disturbances (i.e., a change in disturbance in response to a change in climate). Due to conceptual advances in disturbance ecology in the 1980s [3,21] and the increasing availability of climate scenario data and remotely sensed information we chose to focus our analysis on research emerging from the year 1990 onwards. Material was selected by searching for our six focal disturbance agents (i.e., fire, drought, wind, snow & ice, insects, and pathogens) or applicable aliases (e.g., bark beetles or defoliators for the insects category), in combination with the terms climate and/ or climatic change in the title, abstract, and/ or key words of published papers. In the context of drought it is important to note that we here applied an ecological definition rather than a meteorological one, i.e., we focused on events of severe water limitation that affect ecosystem structure and functioning, and thus fall under the definition of ecological disturbance. After initially screening the abstracts of several thousands of papers, studies not directly addressing climatic controls of disturbances (e.g., work describing disturbance patterns but not their climatic drivers), and those unrelated to the subject matter (e.g., work on insect species that are reproducing in dead trees and are thus not acting as disturbance agent) were excluded, and 674 papers were selected for detailed review. As individual papers frequently contained evidence for more than one climatic effect on disturbances, 1,669 observations were extracted from the selected papers (see Supplementary Text as well as Table S1, and Figure S1-S2 in the Supplementary Information). We conducted an in-depth uncertainty analysis of the information synthesized from the literature, assessing how well the data corresponded with the variable of interest in our analysis (i.e., disturbance activity and changes therein), and evaluating the methodological rigor applied in its generation (see Supplementary Text, Figures S3-S5). We subsequently omitted information that we deemed to be a poor proxy for disturbance change or of limited methodological rigor, resulting in 1,621 observations available for analysis (Supplementary Dataset 1).

We applied a common analysis scheme to all reviewed papers. For each paper we recorded meta-data on study location, methodological approach (i.e., empirical, experimental, or simulation-based), and the disturbance agent(s) studied. We distinguished direct, indirect, and interaction effects [41–43] of climate change on disturbances in our analysis of the literature. Direct effects were defined as the unmediated impacts of climate variables on disturbance processes. Examples included changes in the frequency or severity of wind events and drought periods, changes in lightning activity, or climate-mediated changes in the metabolic rates of pests and pathogens. Indirect effects were defined as changes in the disturbance regime through climate effects on vegetation and other ecosystem processes not directly related to disturbances. Prominent processes considered here are climate-mediated changes in the tree population and community composition, and include an alteration of the disturbance susceptibility through a change in tree species composition, size, density (e.g., fuel available for burning), and distribution, as well as changes in tree-level vulnerability (e.g., changes in soil anchorage of trees against wind due to variation in soil frost). Interaction effects were defined as linked or compounding relationships between disturbance agents [27], such as an increased risk of bark beetle outbreaks resulting from wind disturbance (creating large amounts of effectively defenseless breeding material supporting the build-up of beetle population) or drought (weakening tree defenses against beetles). Only interactions between the six agents investigated here were considered explicitly.

To characterize the climate sensitivity of disturbances we first collated the evidence for direct, indirect, and interaction effects of climate change for each of the six disturbance agents studied. We screened the information for key climatic drivers of disturbances, and analyzed their variation over biomes. As an auxiliary variable we determined the response time of the ecosystem (i.e., the time needed to respond to a respective change in a climate driver) on an ordinal scale. Subsequently, we synthesized the literature regarding potential future changes in the disturbance regime. This analysis was conducted at two levels: First, the sign of the climate effect (i.e., positive: more disturbance, negative: less disturbance) in response to changes in the respective climate variable(s) was assessed. Interaction effects were grouped by directionality (links between individual agents) and also analyzed for the sign of the interaction. This information was synthesized qualitatively, scrutinizing whether amplifying or dampening climate change impacts prevail for each disturbance agent (Figure S6). We conducted this analysis separately for two broad trajectories of change: (1) Warmer and wetter conditions, which assume an increase in both indicators of the thermal environment and water availability (e.g., warmer temperatures, higher levels of precipitation and soil moisture, or lower levels of water deficit and drought indices), and (2) warmer and drier conditions, with an opposite direction of change for indicators of water availability under warming temperatures (see Supplementary Text for details). Second, we calculated a relative effect size (disturbance change in response to future climate change relative to baseline climate conditions, with a value of one indicating no change) across all the potential future climate conditions studied in the literature. Relative effect sizes were tested against the null hypothesis of no change in disturbance as a result of climate change using Wilcoxon signed rank sum tests. All analyses were conducted using the R language and environment for statistical computing [44], specifically employing the packages circlize [45] and fsmb [46].

Pathways of climate influence

We found evidence for a substantial influence of climate on disturbances via all three scrutinized pathways, i.e., direct, indirect, and interaction effects. More than half of the observations reported in the literature related to direct climate effects (57.1%), which were the most prominent pathway of climate influence for all analyzed agents except insects (Figure 1). Direct effects were found to be particularly pronounced for abiotic agents: Abiotic disturbances often are the direct consequence of climatic extremes, and are thus highly sensitive to changes in their occurrence, intensity, and duration (Table 1). Furthermore, 25.0% of the analyzed observations reported indirect effects of climate change on disturbances. Climate-mediated changes in forest structure and composition were particularly relevant in the context of wind disturbance. Also interactions between disturbance agents are well documented in the analyzed literature (17.9% of the overall observations). For insects, for instance, 40.8% of the reported effects were associated with disturbance interactions. Links between abiotic (influencing agent) to biotic (influenced agent) disturbances were found to be particularly strong (Figure 2a). The large majority of the recorded interaction effects were positive or predominately positive (71.0%), indicating an amplification of disturbance as a result of the interaction between agents. In particular, disturbances by drought and wind strongly facilitate the activity of other disturbance agents, such as insects and fire (Figure 2b, Table S2). Overall, only 16.2% of the studies on disturbance interactions reported a negative or predominately negative (i.e., dampening) effect between interacting disturbance agents.

Climate drivers and response times

The climatic drivers of disturbances varied strongly with agent and region. However, temperature-related variables were the most prominent climatic drivers reported in the forest disturbance literature (42.0%). Water availability was a second important climatic influence on disturbance regimes (37.9%). The importance of temperature-related variables on the disturbance regime increased with latitude and was highest in the boreal biome (Figure S9). Conversely, the importance of water availability decreased with latitude and was highest in the tropics. In addition to temperature and water availability, a wide range of other climate-related variables were associated with disturbance change, ranging from wind speed and atmospheric moisture content to snow pack and atmospheric CO_2 concentration.

The response times of the disturbance regime to changes in the climate system varied widely, ranging from annual to centennial scales. Response times were clearly related to the type of climate effect, with disturbance interactions constituting the fastest responding pathway and indirect effects being the slowest (Figure S10). For interaction effects, the analyzed literature reports a response time of <6 years in 81.0% of the reviewed cases, and only 9.0% of the studied interaction effects have a response time of >25 years. For indirect effects, only 38.6% of the systems responded within the first five years of the respective climatic forcing, while 44.6% of the responses took >25 years.

Potential future disturbance change

At the global scale, our analysis suggests that disturbances from five out of the six analyzed agents are likely to increase in a warming world. The exception are disturbances from snow & ice, which are likely to decrease in the future, especially under warmer and drier conditions (Figure S7, S11). For warmer and dryer future conditions, the large majority of studies suggested an increase in fires (82.4% of the observations), drought (74.2%), and insect activity (78.4%) (Figure 3). Under warmer and wetter conditions, on the other hand, the evidence for increased activity from these disturbance agents was significantly reduced (55.0%, 51.2%, and 65.3%, respectively). Wetter conditions were found to particularly foster wind disturbance (expected to increase in 89.1% of the cases) and pathogen activity (69.0%). Indirect climate effects were dampening the overall climate sensitivity of the system more often than direct climate effects (Table S2, Figures S7-S8), although no significant differences in effect sizes were found (Figure S13). Interaction effects were largely amplifying climate sensitivity (Figure 2).

Across all scenarios considered in the analyzed literature, the ratio between disturbances under future climate to disturbances under baseline conditions was significantly positive ($p<0.05$). The exception were disturbances from snow & ice, which decreased significantly (median effect size of 0.345 over all studies and climate change scenarios, see Figure S11). Disturbances from all other agents increased under future climate change, with median effect sizes of between 1.34 and 1.51. Climate-related disturbance effects were positive across all biomes ($p<0.001$) and moderately increased with latitude (Figure S12), with the highest values reported for the boreal zone (1.71). Furthermore, coniferous forests had a significantly higher future disturbance effect size than broadleaved and mixed forest types (Figure S14). Also, longer response times of disturbances to climate change were associated with elevated effect sizes (Figure S15).

Discussion and conclusion

We found strong support for the hypothesis that climate change could markedly modify future forest disturbance regimes at the global scale. Our analysis of the global forest disturbance literature suggests that particularly disturbances from fire, insects, and pathogens are likely to increase in a warming world (regardless of changes in water availability). These agents and their interactions currently dominate disturbance regimes in many forests of the world, and will likely gain further importance globally in the coming decades. Future changes of disturbances caused by other agents such as drought, wind, and snow will be strongly contingent on changes in water availability, which can be expected to vary more strongly locally and intra-annually than temperature changes. Wind disturbance, for instance, which is currently the most important disturbance agent in Europe [40], is expected to respond more strongly to changes in precipitation (and the corresponding changes in tree soil anchorage and tree growth) than to warming temperatures (cf. Figure 3a,b). Yet the most influential climate variable determining wind disturbance remains the frequency and intensity of strong winds, for which current and future trends remain inconclusive [47,48]. In general, our global summary of the climate sensitivity of forest disturbance regimes suggests that the recently observed increases in disturbance activity [10,40,49] are likely to continue in the coming decades as climate warms further [50,51].

Our synthesis of effect pathways showed that direct climate effects were by far the most prominently reported impact in the analyzed literature. This underlines the importance of climatic drivers as inciting factors of tree mortality, and highlights the strong dependence of developmental rates of biotic disturbance agents on climatic conditions [26,35]. However, the prominence of direct effects in the literature may at least partially result from the fact that they are easier to study and isolate (e.g., in laboratory experiments [52]) than indirect and interaction effects. Publication bias might thus result in an overestimation of the importance of direct effects relative to indirect and interaction effects in our analysis.

Indirect effects, mediated by climate-related changes in vegetation structure and composition, were most frequently reported for wind disturbance, but were documented in the literature for all six studied disturbance agents. They are slower than climate effects via direct and interaction pathways, with response times frequently in the range of several decades. Also, indirect effects are often dampening disturbance increases (Table S2, Figures S7-S8), e.g., when trees susceptible to an increasingly aggressive insect pest are outcompeted by individuals or species better adapted to warmer climates, resulting in a system less vulnerable to disturbances [33,53]. A second important class of dampening indirect effects occur when a previous disturbance event lowers the probability for subsequent disturbances by the same agent, e.g., through a disturbance-induced alteration of forest structure or the depletion of the resource a disturbance agent depends upon [54–56]. The temporal mismatch observed between direct and indirect effects (Figure S10) suggests that disturbances will likely increase further in the coming decades, as dampening effects of changes in forest structure and composition take effect only with considerable delay. Here it has to be noted that our estimate of response times to climatic changes is necessarily truncated by the observation periods of the underlying studies. It might thus be biased against long-term effects [8] and underestimate the full temporal extent of climate effects on disturbances.

Evidence for potential changes in disturbance interactions was found for all six investigated agents. In this context it is noteworthy that the large majority of the interaction effects reported in the literature are positive, i.e., amplifying disturbance activity. We showed that interactions are especially important for the dynamics of biotic disturbance agents. As an increasing disturbance activity under climate change also means an increasing propensity for disturbance interactions, biotic agents could be particularly prone to further intensification via the influence of other disturbance agents [29,57]. This is of growing concern as amplification of disturbances through interactions could also increase the potential for the exceedance of ecological thresholds and tipping points [27,58].

Particularly indirect and interaction effects of climate change on disturbance regimes need to be better understood to comprehensively assess future trajectories of disturbance in a changing world. The complexity of disturbance interactions complicates predictions of future forest change, and highlights the need for further research comprising multiple interacting disturbance agents and larger spatiotemporal scales. Dynamic vegetation models are prime tools for this domain of inquiry [59]. Simulation models are able to consistently track vegetation

– disturbance feedbacks over time frames of decades to centuries [33,60], and allow controlled experiments to isolate the effects of interactions between different agents [32,60]. However, many current disturbance models either do not explicitly consider vegetation processes, or disturbance agents are simulated in isolation, neglecting potential interaction effects. Future work should thus focus on integrating disturbance and vegetation dynamics in models, in order to address the complex interrelations between climate, vegetation, and disturbance [61,62]. Furthermore, long-term ecological observations and dedicated experimentation are needed to improve our understanding of changing disturbance regimes, and provide the data needed for parameterizing and evaluating the above mentioned simulation models [59].

Our analysis revealed a strong bias of the literature towards agents such as fire, drought, insects, and pathogens, as well as ecosystems located in North America and Europe (Table S1, Figure S1). However, climate change is a global phenomenon, affecting forests in all regions of the world. To obtain a more comprehensive understanding of the global patterns of disturbance change, considerable knowledge gaps on the climate sensitivity of disturbance regimes need to be filled. It remains unclear, for instance, if the increasing effect of future climate change with latitude reported here (Figure S9) is the result of an increased exposure of boreal forests to climate change in combination with naturally lower tree species diversity, or whether it is simply the effect of a publication bias towards these ecosystems. Furthermore, the fact that disturbance research is currently focused on a limited number of agents could be increasingly problematic in the future, as agents that were of little regional relevance in the past could gain importance under changing climatic conditions. In this regard it should be noted that invasive alien pests [63,64] were not in the focus of our analysis, but are likely to contribute considerably to future changes in disturbance regimes.

Climate-induced changes in disturbance regimes are a major challenge for the sustainable provisioning of ecosystem services to society [6,14]. Our finding of prominent indirect effects suggests that forest management can actively modulate the climate sensitivity of disturbance regimes via modifying forest structure and composition. However, mitigating the direct effects of a changing climate through management will be rarely possible, which suggests that future management will need to find ways of coping with disturbance change. A promising approach in this regard is to foster the resilience of forests to changing disturbance regimes, enabling their recovery from and adaptation to disturbances [17,65], in order to ensure a continuous provisioning of ecosystem services [18], and ultimately prepare both ecosystems and society for an increasingly disturbed future of forests.

Acknowledgements

This work is the result of a working group within the EU COST Action PROFOUND (FP1304) and the IUFRO Task Force on Climate Change and Forest Health. R. Seidl acknowledges funding from a START grant of the Austrian Science Fund FWF (Y 895-B25). M. Kautz acknowledges funding from the EU FP7 project LUC4C, grant 603542. M. Peltoniemi was funded by EU Life+ (LIFE12 ENV/FI/000409). C.P.O. Reyer acknowledges funding from the German Federal Ministry of Education and Research (BMBF, grant no. 01LS1201A1). D. Martin-Benito was funded by a Marie-Curie IEF Grant (EU-Grant 329935). J. Wild was funded by the long-term research and development project RVO 67985939 (The Czech Academy of Sciences). M. Svoboda, V. Trotsiuk and J. Wild acknowledge support by a project of the Ministry of Education, Youth and Sports no. LD15158. M. Petr acknowledges funding support from Forestry Commission (UK) funded research on climate change impacts. J. Honkaniemi acknowledges funding from the Foundation for Research of Natural Resources in Finland, grant no. 2015090. M. Svoboda and V. Trotsiuk acknowledge funding from the project GAČR 15-14840S. We thank four anonymous reviewers for helpful comments on an earlier version of the manuscript.

Author contributions

R. Seidl and C.P.O. Reyer initiated the research. R. Seidl and D. Thom designed the study, with feedback from authors during workshops in Vienna, Austria (April 2015) and Novi Sad, Serbia (November 2015). G. Vacchiano, D. Ascoli, P. Mairota, C.P.O. Reyer, and R. Seidl reviewed the fire literature. D. Martin-Benito, M. Petr, and V. Trotsiuk reviewed the drought literature. J. Wild, M.J. Lexer, M. Fabrika, and T. Nagel reviewed the wind literature. D. Thom and T. Nagel reviewed the snow & ice literature. M. Kautz, D. Thom, M.J. Lexer, M. Svoboda, and J. Wild reviewed the literature on insects. M. Peltoniemi, J. Honkaniemi, and M. Petr reviewed the literature on pathogens. R. Seidl conducted the analyses. All authors contributed to writing and revising the manuscript.

Additional information

Supplementary information is available in the online version of the paper.

References

1. Turner, M. G. Disturbance and landscape dynamics in a changing world. *Ecology* **91,** 2833–2849 (2010).

2. Frelich, L. E. *Forest dynamics and disturbance regimes. Studies from temperate evergreen - deciduous forests*. (Cambridge University Press, 2002).

3. White, P. S. & Pickett, S. T. A. in *The ecology of natural disturbance and patch dynamics* (eds. Pickett, S. T. A. & White, P. S.) 3–13 (Academic Press, 1985).

4. Turner, M. G., Tinker, D. B., Romme, W. H., Kashian, D. M. & Litton, C. M. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* **7,** 751–775 (2004).

5. Beudert, B. *et al.* Bark beetles increase biodiversity while maintaining drinking water quality. *Conserv. Lett.* **8,** 272–281 (2015).

6. Thom, D. & Seidl, R. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biol. Rev.* **91,** 760–781 (2016).

7. Holling, C. S. & Gunderson, L. H. in *Panarchy. Understanding the transformations in*

human and natural systems (eds. Gunderson, L. H. & Holling, C. S.) 25–62 (Island Press, 2002).

8. Thom, D., Rammer, W. & Seidl, R. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. *Glob. Chang. Biol.* **23,** 269–282 (2017).

9. Seidl, R., Schelhaas, M.-J. & Lexer, M. J. Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Glob. Chang. Biol.* **17,** 2842–2852 (2011).

10. Westerling, A. L. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **371,** 20150178 (2016).

11. Pechony, O. & Shindell, D. T. Driving forces of global wildfires over the past millennium and the forthcoming century. *Proc. Natl. Acad. Sci. U. S. A.* **107,** 19167–19170 (2010).

12. Paritsis, J. & Veblen, T. T. Dendroecological analysis of defoliator outbreaks on Nothofagus pumilio and their relation to climate variability in the Patagonian Andes. *Glob. Chang. Biol.* **17,** 239–253 (2011).

13. Kautz, M., Meddens, A. J. H., Hall, R. J. & Arneth, A. Biotic disturbances in Northern Hemisphere forests – a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. *Glob. Ecol. Biogeogr.* **in press,** (2016).

14. Millar, C. I. & Stephenson, N. L. Temperate forest health in an era of emerging megadisturbance. *Science* **349,** 823–826 (2015).

15. Allen, C. D., Breshears, D. D. & McDowell, N. G. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6,** art129 (2015).

16. Reyer, C. P. O. *et al.* Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. *J. Ecol.* **103,** 5–15 (2015).

17. Johnstone, J. F. *et al.* Changing disturbance regimes, climate warming and forest resilience. *Front. Ecol. Environ.* **14,** 369–378 (2016).

18. Seidl, R., Spies, T. A., Peterson, D. L., Stephens, S. L. & Hicke, J. A. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *J. Appl. Ecol.* **53,** 120–129 (2016).

19. Lindner, M. *et al.* Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manage.* **259,** 698–709 (2010).

20. White, P. S. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* **45,** 229–299 (1979).

21. Sousa, W. P. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* **15,** 353–391 (1984).

22. Dale, V. H. *et al.* Climate change and forest disturbances. *Bioscience* **51,** 723–734 (2001).

23. Overpeck, J. T., Rind, D. & Goldberg, R. Climate induced changes in forest disturbance and vegetation. *Nature* **343,** 51–53 (1990).

24. Williams, A. P. & Abatzoglou, J. T. Recent advances and remaining uncertainties in resolving past and future climate effects on global fire activity. *Curr. Clim. Chang. Reports* **2,** 1–14 (2016).

25. Raffa, K. F. *et al.* in *Climate change and insect pests* (eds. Björkman, C. & Niemelä, P.) 173–201 (CABI, 2015).

26. Sturrock, R. N. *et al.* Climate change and forest diseases. *Plant Pathol.* **60,** 133–149 (2011).

27. Buma, B. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* **6,** art70 (2015).

28. Foster, C. N., Sato, C. F., Lindenmayer, D. B. & Barton, P. S. Integrating theory into disturbance interaction experiments to better inform ecosystem management. *Glob. Chang. Biol.* **22,** 1325–1335 (2016).

29. Jactel, H. *et al.* Drought effects on damage by forest insects and pathogens: a meta-analysis. *Glob. Chang. Biol.* **18,** 267–276 (2012).

30. Peters, D. P. C. *et al.* Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* **2,** art81 (2011).

31. Berrang-Ford, L., Pearce, T. & Ford, J. D. Systematic review approaches for climate change adaptation research. *Reg. Environ. Chang.* **15,** 755–769 (2015).

32. Seidl, R. & Rammer, W. Climate change amplifies the interactions between wind and bark beetle disturbance in forest landscapes. *Landsc. Ecol.* **in press,** doi:10.1007/s10980-016-0396-4 (2016).

33. Temperli, C., Bugmann, H. & Elkin, C. Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. *Ecol. Monogr.* **83,** 383–402 (2013).

34. Flannigan, M. *et al.* Global wildland fire season severity in the 21st century. *For. Ecol. Manage.* **294,** 54–61 (2013).

35. Jönsson, A. M. *et al.* Modelling the potential impact of global warming on Ips typographus voltinism and reproductive diapause. *Clim. Change* **109,** 695–718 (2011).

36. Hanewinkel, M., Cullmann, D. A., Schelhaas, M.-J., Nabuurs, G.-J. & Zimmermann, N. E. Climate change may cause severe loss in the economic value of European forest land. *Nat. Clim. Chang.* **3,** 203–207 (2013).

37. Schröter, D. *et al.* Ecosystem service supply and vulnerability to global change in Europe. *Science* **310,** 1333–1337 (2005).

38. Naudts, K. *et al.* Europe’s forest management did not mitigate climate warming. *Science* **351,** 597–601 (2016).

39. Running, S. W. Ecosystem disturbance, carbon, and climate. *Science* **321,** 652–653 (2008).

40. Seidl, R., Schelhaas, M.-J., Rammer, W. & Verkerk, P. J. Increasing forest disturbances in Europe and their impact on carbon storage. *Nat. Clim. Chang.* **4,** 806–

810 (2014).

41. Clark, J. S., Bell, D. M., Kwit, M. C. & Zhu, K. Competition-interaction landscapes for the joint response of forests to climate change. *Glob. Chang. Biol.* **20,** 1979–1991 (2014).

42. Bentz, B. J. *et al.* Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *Bioscience* **60,** 602–613 (2010).

43. Liu, Z. & Wimberly, M. C. Direct and indirect effects of climate change on projected future fire regimes in the western United States. *Sci. Total Environ.* **542,** 65–75 (2016).

44. R Development Core Team. *R: A language and environment for statistical computing*. (R Foundation for Statistical Computing, 2016).

45. Gu, Z., Gu, L., Eils, R., Schlesner, M. & Brors, B. circlize implements and enhances circular visualization in R. *Bioinformatics* **30,** 2811–2812 (2014).

46. Nakazawa, M. fmsb: Functions for medical statistics book with some demographic data. R package version 0.5.1. *http://CRAN.R-project.org/package=fmsb* (2014).

47. Knutson, T. R. *et al.* Tropical cyclones and climate change. *Nat. Geosci.* **3,** 157–163 (2010).

48. Bender, M. A. *et al.* Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. *Science* **327,** 454–458 (2010).

49. Meddens, A. J. H., Hicke, J. A. & Ferguson, C. A. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecol. Appl.* **22,** 1876–1891 (2012).

50. IPCC. *Climate Change 2013: The physical science basis. Working Group I contribution to the IPCC fifth assessment report.* (Intergovernmental Panel on Climate Change, Cambridge University Press, 2013).

51. Solomon, S., Plattner, G.-K., Knutti, R. & Friedlingstein, P. Irreversible climate change due to carbon dioxide emissions. *Proc. Natl. Acad. Sci. U. S. A.* **106,** 1704–1709 (2009).

52. Müller, M. M. *et al.* Predicting the activity of Heterobasidion parviporum on Norway spruce in warming climate from its respiration rate at different temperatures. *For. Pathol.* **44,** 325–336 (2014).

53. Cruickshank, M. G., Jaquish, B. & Nemec, A. F. L. Resistance of half-sib interior Douglas-fir families to Armillaria ostoyae in British Columbia following artificial inoculation. *Can. J. For. Res.* **40,** 155–166 (2010).

54. Panferov, O., Doering, C., Rauch, E., Sogachev, A. & Ahrends, B. Feedbacks of windthrow for Norway spruce and Scots pine stands under changing climate. *Environ. Res. Lett.* **4,** 45019 (2009).

55. Cowden, M. M., Hart, J. L., Schweitzer, C. J. & Dey, D. C. Effects of intermediate-scale wind disturbance on composition, structure, and succession in Quercus stands: Implications for natural disturbance-based silviculture. *For. Ecol. Manage.* **330,** 240–251 (2014).

56. Seidl, R., Donato, D. C., Raffa, K. F. & Turner, M. G. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. *Proc. Natl. Acad. Sci. U. S. A.* **113,** 13075–13080 (2016).

57. Stadelmann, G., Bugmann, H., Wermelinger, B. & Bigler, C. Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. *For. Ecol. Manage.* **318,** 167–174 (2014).

58. Paine, R. T., Tegner, M. J. & Johnson, E. A. Compounded perturbations yield ecological surprises. *Ecosystems* **1,** 535–545 (1998).

59. Becknell, J. M. *et al.* Assessing interactions among changing climate, management, and disturbance in forests: A macrosystems approach. *Bioscience* **65,** 263–274 (2015).

60. Temperli, C., Veblen, T. T., Hart, S. J., Kulakowski, D. & Tepley, A. J. Interactions among spruce beetle disturbance, climate change and forest dynamics captured by a forest landscape model. *Ecosphere* **6,** art231 (2015).

61. Seidl, R. *et al.* Modelling natural disturbances in forest ecosystems: a review. *Ecol. Modell.* **222,** 903–924 (2011).

62. Keane, R. E. *et al.* Representing climate, disturbance, and vegetation interactions in landscape models. *Ecol. Modell.* **309–310,** 33–47 (2015).

63. Valenta, V., Moser, D., Kuttner, M., Peterseil, J. & Essl, F. A high-resolution map of emerald ash borer invasion risk for southern central Europe. *Forests* **6,** 3075–3086 (2015).

64. Gandhi, K. J. K. & Herms, D. A. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biol. Invasions* **12,** 389–405 (2010).

65. Seidl, R. The shape of ecosystem management to come: Anticipating risks and fostering resilience. *Bioscience* **64,** 1159–1169 (2014).

66. Billmire, M., French, N. H. F., Loboda, T., Owen, R. C. & Tyner, M. Santa Ana winds and predictors of wildfire progression in southern California. *Int. J. Wildl. Fire* **23,** 1119–1129 (2014).

67. Pausas, J. G. & Ribeiro, E. The global fire-productivity relationship. *Glob. Ecol. Biogeogr.* **22,** 728–736 (2013).

68. Bowman, D. M., Murphy, B. P., Williamson, G. J. & Cochrane, M. A. Pyrogeographic models, feedbacks and the future of global fire regimes. *Glob. Ecol.* **32,** 821–824 (2014).

69. Ryan, K. C. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fenn.* **36,** 13–39 (2002).

70. Cook, B. I., Smerdon, J. E., Seager, R. & Coats, S. Global warming and 21st century drying. *Clim. Dyn.* **43,** 2607–2627 (2014).

71. Suarez, M. L. & Kitzberger, T. Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests. *Can. J. For. Res.* **38,** 3002–3010 (2008).

72. Harvey, B. J., Donato, D. C. & Turner. High and dry: Postfire drought and large stand-replacing burn patches reduce postfire tree regeneration in subalpine forests. *Glob. Ecol. Biogeogr.* **25,** 655–669 (2016).

73. Donat, M. G., Leckebusch, G. C., Wild, S. & Ulbrich, U. Future changes in European winter storm losses and extreme wind speeds inferred from GCM and RCM multi-model simulations. *Nat. Hazards Earth Syst. Sci.* **11,** 1351–1370 (2011).

74. Peltola, H. *et al.* Impacts of climate change on timber production and regional risks of wind-induced damage to forests in Finland. *For. Ecol. Manage.* **260,** 833–845 (2010).

75. Usbeck, T. *et al.* Increasing storm damage to forests in Switzerland from 1858 to 2007. *Agric. For. Meteorol.* **150,** 47–55 (2010).

76. Moore, J. R. & Watt, M. S. Modelling the influence of predicted future climate change on the risk of wind damage within New Zealand's planted forests. *Glob. Chang. Biol. Biol.* **21,** 3021–3035 (2015).

77. Whitney, R. D., Fleming, R. L., Zhou, K. & Mossa, D. S. Relationship of root rot to black spruce windfall and mortality following strip clear-cutting. *Can. J. For. Res.* **32,** 283–294 (2002).

78. Teich, M., Marty, C., Gollut, C., Grêt-Regamey, A. & Bebi, P. Snow and weather conditions associated with avalanche releases in forests: Rare situations with decreasing trends during the last 41years. *Cold Reg. Sci. Technol.* **83,** 77–88 (2012).

79. Gregow, H., Peltola, H., Laapas, M., Saku, S. & Venäläinen, A. Combined occurrence of wind , snow loading and soil frost with implications for risks to forestry in Finland under the current and changing climatic conditions. *Silva Fenn.* **45,** 35–54 (2011).

80. Cheng, C. S., Auld, H., Li, G., Klaassen, J. & Li, Q. Possible impacts of climate change on freezing rain in south-central Canada using downscaled future climate scenarios. *Nat. Hazards Earth Syst. Sci.* **7,** 71–87 (2007).

81. Kilpeläinen, A. *et al.* Impacts of climate change on the risk of snow-induced forest damage in Finland. *Clim. Change* **99,** 193–209 (2010).

82. Bebi, P., Kulakowski, D. & Rixen, C. Snow avalanche disturbances in forest ecosystems—State of research and implications for management. *For. Ecol. Manage.* **257,** 1883–1892 (2009).

83. Maroschek, M., Rammer, W. & Lexer, M. J. Using a novel assessment framework to evaluate protective functions and timber production in Austrian mountain forests under climate change. *Reg. Environ. Chang.* **15,** 1543–1555 (2015).

84. Lemoine, N. P., Burkepile, D. E. & Parker, J. D. Variable effects of temperature on insect herbivory. *PeerJ* **2,** e376 (2014).

85. Battisti, A. *et al.* Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol. Appl.* **15,** 2084–2096 (2005).

86. Evangelista, P. H., Kumar, S., Stohlgren, T. J. & Young, N. E. Assessing forest vulnerability and the potential distribution of pine beetles under current and future climate scenarios in the Interior West of the US. *For. Ecol. Manage.* **262,** 307–316 (2011).

87. Schwartzberg, E. G. *et al.* Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia* **175,** 1041–1049 (2014).

88. Gaylord, M. L. *et al.* Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytol.* **198,** 567–78 (2013).

89. Aguayo, J., Elegbede, F., Husson, C., Saintonge, F.-X. & Marçais, B. Modeling climate impact on an emerging disease, the Phytophthora alni-induced alder decline. *Glob. Chang. Biol.* **20,** 3209–3221 (2014).

90. Vacher, C., Vile, D., Helion, E., Piou, D. & Desprez-Loustau, M.-L. Distribution of parasitic fungal species richness: influence of climate versus host species diversity. *Divers. Distrib.* **14,** 786–798 (2008).

91. Karnosky, D. F. *et al.* Interacting elevated CO2 and tropospheric O3 predisposes aspen (Populus tremuloides Michx.) to infection by rust (Melampsora medusae f. sp. tremuloidae). *Glob. Chang. Biol.* **8,** 329–338 (2002).

92. Garnas, J. R., Houston, D. R., Ayres, M. P. & Evans, C. Disease ontogeny overshadows effects of climate and species interactions on population dynamics in a nonnative forest disease complex. *Ecography* **35,** 412–421 (2012).

93. Tsui, C. K. M. *et al.* Population structure and migration pattern of a conifer pathogen, Grosmannia clavigera, as influenced by its symbiont, the mountain pine beetle. *Mol. Ecol.* **21,** 71–86 (2012).

Tables

Table 1: Important processes through which climate influences forest disturbances.

Disturbance agent	Direct effects: Climate impact through changes in…	Indirect effects: Climate impact through changes in…	Interaction effects: Climate impact through changes in…
Fire	Fuel moisture [24] Ignition (e.g., lightning activity) Fire spread (e.g., wind speed [66])	Fuel availability (e.g., vegetation productivity [67]) Flammability (e.g., vegetation composition) Fuel continuity (e.g., vegetation structure [68])	Fuel availability (e.g., via wind or insect disturbance) Fuel continuity (e.g., avalanche paths as fuel breaks [69])
Drought	Occurrence of water limitation Duration of water limitation [70] Intensity of water deficit [70]	Water use and water use efficiency (e.g., tree density and competition) Susceptibility to water deficit (e.g., tree species composition [71])	Water use and water use efficiency (e.g., insect-related density changes) Susceptibility to water deficit (e.g., fire-mediated changes in forest structure [72])
Wind	Occurrence of strong winds [73] Duration of wind events [74] Intensity of wind events (e.g., peak wind speeds) [75]	Tree anchorage (e.g., soil frost [75]) Wind exposure (e.g., tree growth [76]) Wind resistance (e.g., tree species composition [54])	Wind exposure (e.g., insect disturbances increases canopy roughness) Soil anchorage (e.g., pathogens decrease rooting stability [77]) Resistance to stem breakage (e.g., pathogens decrease stability)
Snow & Ice	Snow occurrence [78] Snow duration [79] Occurrence of freezing rain [80]	Exposure of forest to snow [81] Avalanche risk [82]	Avalanche risk (e.g., through gap formation by bark beetles [83])

Insects	Agent metabolic rate (e.g., reproduction [35]) Agent behavior (e.g., consumption [84]) Agent survival [85]	Host distribution and range [86] Agent - host synchronization (e.g., budburst [87]) Host defense (e.g., carbohydrate reserves)	Host presence and abundance [33] Host resistance and defense (e.g., through changes in drought [88])
Pathogens	Agent metabolic rate (e.g., respiration [52]) Agent abundance [89]	Host abundance and diversity [90] Host defense [91]	Agent interaction and asynchrony [92] Agent dispersal (e.g., through vector insects [93])

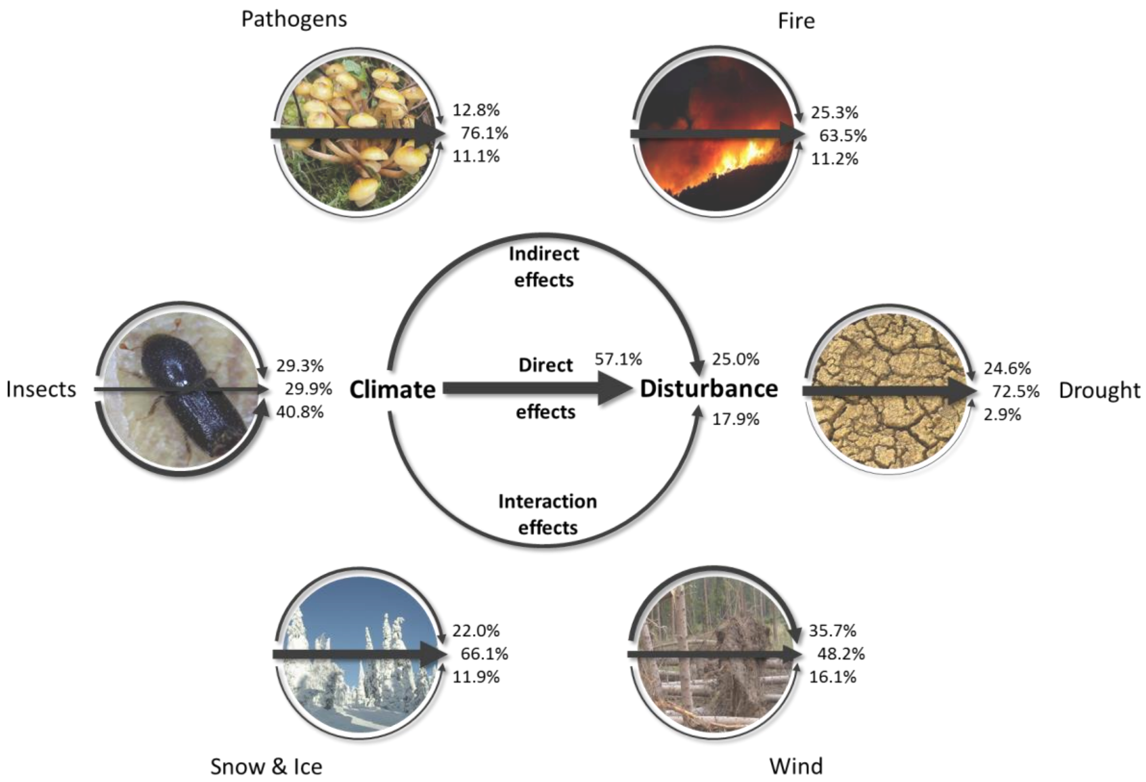

Figure 1: Distribution of evidence for direct, indirect, and interaction effects of climate change on forest disturbance agents in the reviewed literature. For every agent, arrow widths and percentages indicate the relative prominence of the respective effect as expressed by the number of observations extracted from the analyzed literature supporting it. The central panel displays the aggregate result over all disturbance agents. Direct effects are unmediated impacts of climate on disturbance processes, while indirect effects describe a climate influence on disturbances through effects on vegetation and other ecosystem processes. Interaction effects refer to the focal agent being influenced by other disturbance agents. Image credits: Wikimedia Commons.

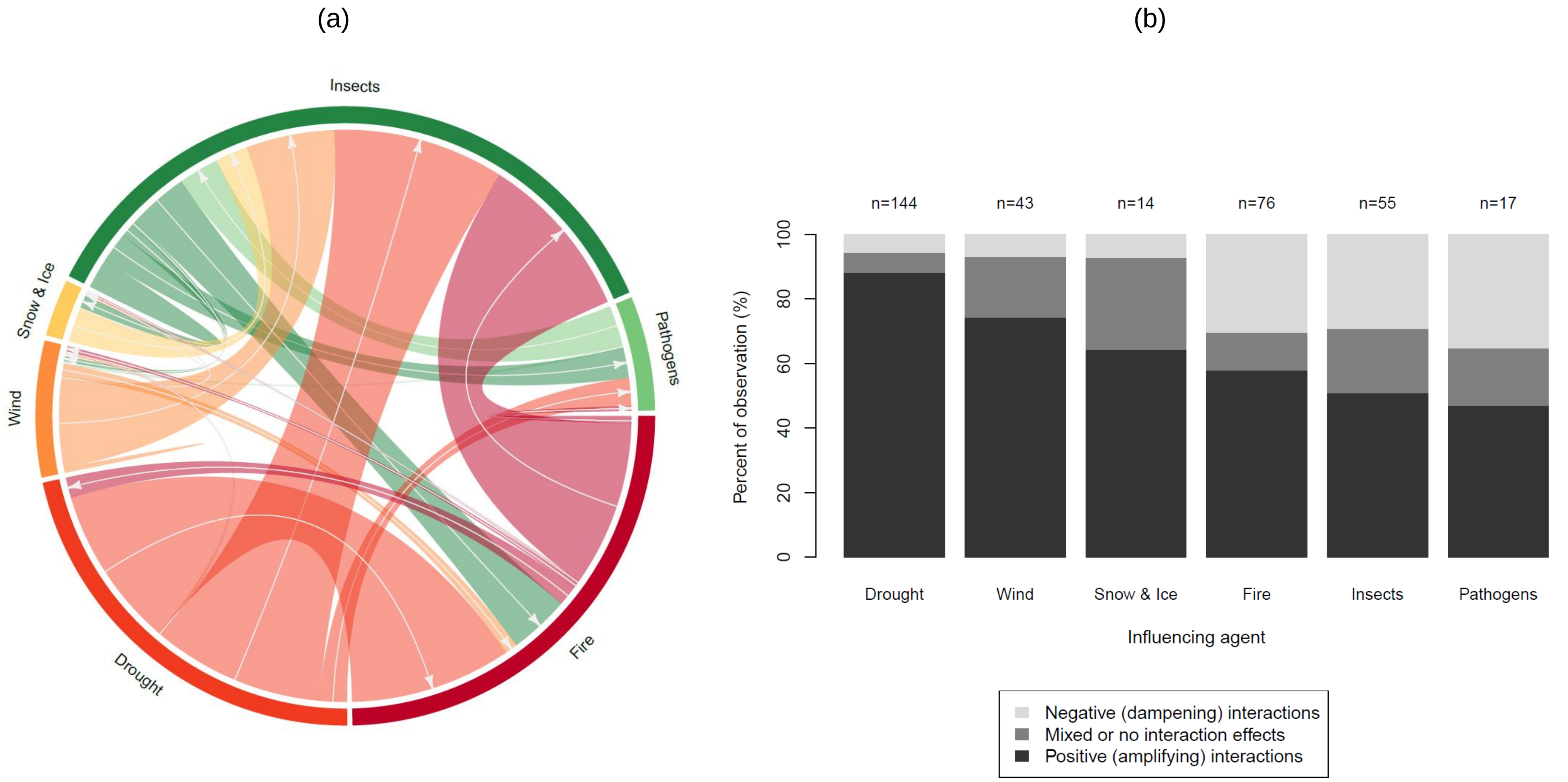

Figure 2: Interactions between forest disturbance agents. (a) The sector size in the outer circle indicates the distribution of interactions over agents, while the flows through the center of the circle illustrate the relative importance of interactions between individual agents (as measured by the number of observations reporting on the respective interaction). Arrows point from the influencing agent to the agent being influenced by the interaction. (b) Sign of the interaction effect induced by the influencing agent on the influenced agent. n= Number of observations.

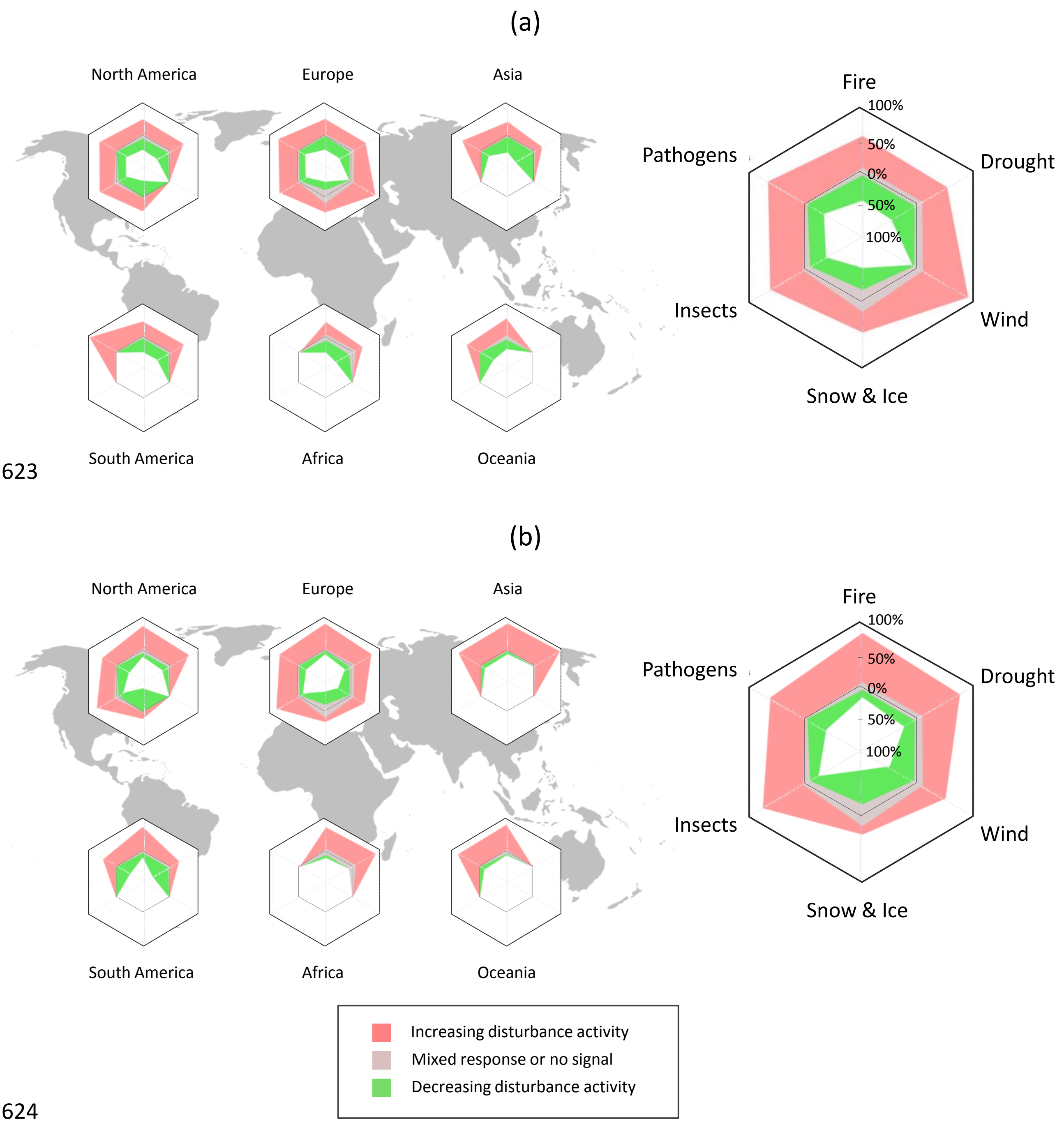

Figure 3: Global disturbance response to changing temperature and water availability. Radar surfaces indicate the distribution of evidence (% of observations) for increasing or decreasing disturbance activity under (a) warmer and wetter as well as (b) warmer and dryer climate conditions. The large radar plot to the right summarizes the responses over all continents. Disturbance agents with less than four observations were omitted in the analysis. Only direct and indirect climate effects are considered here. More details on the qualitative modeling applied can be found in the Supplementary Material.