



RESEARCH ARTICLE

Functional Ecology



Extending the climatological concept of 'Detection and Attribution' to global change ecology in the Anthropocene

Ulf Büntgen^{1,2,3,4} | J. Fidel González-Rouco^{5,6} | Jürg Luterbacher^{7,8} |
Nils Christian Stenseth⁹ | Derek M. Johnson¹⁰

¹Department of Geography, University of Cambridge, Cambridge, UK; ²Swiss Federal Research Institute (WSL), Birmensdorf, Switzerland; ³Global Change Research Institute of the Czech Academy of Sciences (CzechGlobe), Brno, Czech Republic; ⁴Department of Geography, Faculty of Science, Masaryk University, Brno, Czech Republic; ⁵Department of Physics of the Earth & Astrophysics, University Complutense, Madrid, Spain; ⁶Institute of Geosciences IGEO (UCM-CSIC), Madrid, Spain; ⁷Science and Innovation Department, World Meteorological Organization (WMO), Geneva, Switzerland; ⁸Geography Department & Centre for International Development & Environmental Research, Giessen, Germany; ⁹Faculty of Mathematics and Natural Sciences, University of Oslo, Oslo, Norway and ¹⁰Department of Biology, Virginia Commonwealth University, Richmond, VA, USA

Correspondence

Ulf Büntgen

Email: ulf.buentgen@geog.cam.ac.uk;
buentgen@wsl.ch**Funding information**

SustES Project

Handling Editor: Sarah Diamond**Abstract**

1. Research into global change ecology is motivated by the need to understand the role of humans in changing biotic systems. Mechanistic understanding of ecological responses requires the separation of different climatic parameters and processes that often operate on diverse spatiotemporal scales. Yet most environmental studies do not distinguish the effects of internal climate variability from those caused by external, natural (e.g. volcanic, solar, orbital) or anthropogenic (e.g. greenhouse gases, ozone, aerosols, land-use) forcing factors.
2. We suggest extending the climatological concept of 'Detection and Attribution' (DA) to unravel abiotic drivers of ecological dynamics in the Anthropocene. We therefore apply DA to quantify the relative roles of natural versus industrial temperature change on elevational shifts in the outbreak epicentres of the larch budmoth (LBM; *Zeiraphera diniana* or *griseana* Gn.); the classic example of a cyclic forest defoliating insect.
3. Our case study shows that anthropogenic warming shifts the epicentre of travelling LBM waves upward, which disrupts the intensity of population outbreaks that occurred regularly over the past millennium in the European Alps. Our findings demonstrate the ability of DA to detect ecological responses beyond internal system variability, to attribute them to specific external climate forcing factors and to identify climate-induced ecological tipping points.
4. In order to implement the climatological concept of 'Detection and Attribution' successfully into modern global change ecology, future studies should combine high-resolution paleoenvironmental reconstructions and state-of-the-art climate model simulations to inform inference-based ecosystem models.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2020 The Authors. *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

KEYWORDS

anthropogenic climate change, cyclic population dynamics, detection and attribution, global change ecology, inference-based ecological modelling, larch budmoth system

1 | INTRODUCTION

Natural climate variation plays a primary role in shaping the Earth's biotic composition through a multitude of ecological pathways (Cramer et al., 2014). Recent climate change adds anthropogenic forcing to existing natural variability (Masson-Delmotte et al., 2013). To characterize the role of different external forcing factors, climate (and climate change) scientists may use a method called 'Detection and Attribution' (DA; Barnett et al., 1999; Bindoff et al., 2013; Cramer et al., 2014; Hasselmann, 1993; Hegerl et al., 1997, 2010; Hegerl, Crowley, Hyde, & Frame, 2006; Knutson et al., 2017; Knutson, 2017; Rosenzweig & Neofotis, 2013; Schurer et al., 2019; Stone et al., 2013). Detection is defined as the process of demonstrating that climate, or a system affected by climate, has changed in some defined statistical sense without providing a reason for that change. An identified change is detected in observations if its likelihood of occurrence by chance due to internal variability alone is determined to be small, for example, <10% (Hegerl et al., 2010), without necessarily being ascribed to a causal factor. In contrast, attribution is defined as the process of evaluating the relative contribution of multiple causal factors to a change or event with an assignment of statistical confidence. Casual factors usually refer to influences external to the system, which may be of anthropogenic (greenhouse gases, ozone, aerosols, land-use) and/or natural (volcanic eruptions, solar variability, orbital changes) origin (Hegerl et al., 2010). An attributable change refers to a change in which the relative contribution of causal factors has been evaluated along with an assignment of statistical confidence (Bindoff et al., 2013; Hegerl et al., 2010).

Barnett, Pierce, and Schnur (2001), for instance, applied DA to ascribe a significant large-scale warming of the world's oceans over the last five decades to anthropogenic forcing. Similarly, spatial variation in global precipitation patterns during the 20th century (Bindoff et al., 2013; Zhang et al., 2007), and increases in European summer surface temperatures during the same period of time (Christidis et al., 2012; Hegerl et al., 2011), have been associated with a component of man-made climate change through DA analysis. We refer to Rosenzweig and Neofotis (2013) and Cramer et al. (2014) for deeper insights into the DA of anthropogenic climate change impacts. On longer, pre-industrial time-scales, DA has been applied to palaeoclimatic data in order to isolate internal climate variability from external climate forcing (Bindoff et al., 2013; Duan et al., 2019; Hegerl et al., 2007, 2011; Hegerl & Zwiers, 2011; Lean & Rind, 2008; Schurer et al., 2019; Schurer, Hegerl, Mann, Tett, & Phipps, 2013; Schurer, Tett, & Hegerl, 2014; Wang et al., 2017, 2018), and for improving climate model projections to better estimate the future climate sensitivity to different natural (e.g. solar activity, volcanic eruptions, orbital changes) and anthropogenic (e.g. greenhouse

gases, ozone and aerosol emissions, land-use changes) forcing agents (Bindoff et al., 2013; Hegerl, Karl, et al., 2006; Knutson et al., 2017; Lehner, Schurer, Hegerl, Deser, & Frölicher, 2016). The existing literature on DA illustrates its importance for a rigorous comparison of the observed, reconstructed and simulated spatial and temporal distributions of different climatic parameters to gain a mechanistic understanding of the processes involved in shaping our environment. However, the (palaeo)climatic concept of DA has not yet been extended to global change ecology in the Anthropocene.

Here we briefly evaluate some of the major developments in DA during recent years, and propose its conceptual expansion to unravel the relative importance of anthropogenic versus natural climate change for the functioning of ecological systems. For this purpose, we present a case of the larch budmoth (LBM; *Zeiraphera diniana* or *griseana* Gn.), a classic example of regular population cycles over the last millennium. Our example demonstrates the ability of DA to quantify the external impact of anthropogenic and natural climate change on the disruption of regular outbreaks of a forest defoliating insect in the European Alps. We consider our study to be particularly relevant for the emerging field of global change ecology, because the ability to link climatic drivers to biotic responses that deviate from the expected internal system variation is a key to assessing how anthropogenic impacts will affect the productivity and sustainability of a wide range of ecosystems in a warmer future.

2 | MATERIALS AND METHODS**2.1 | Principles of extending DA to ecology**

The ecological effects of anthropogenic climate change are evident across multiple levels in biotic systems, from the performance of biomes down to organismal responses. At the level of population organization, for example, climate-related extinctions and range shifts are well documented in marine and terrestrial environments (Burrows et al., 2011). Biological responses include physiological reactions, which have been studied in both laboratory and field experiments (Feder, 2010). Phenological shifts, for instance, have been detected by comparing modern to historical life-history data (Büntgen, Kauseurud, & Egli, 2012; Cramer et al., 2014; Henne et al., 2018). Meta-analyses may further provide insights into general patterns of biotic responses through the main drivers of global environmental change, including atmospheric CO₂ enrichment, nitrogen deposition, climate, species invasions and land-use/land-cover changes (Tylianakis, Didham, Bascompte, & Wardle, 2008). Although there are many recent examples of what has been introduced as 'Associative Pattern Attribution' (Rosenzweig & Neofotis, 2013) for both terrestrial and marine

systems (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Esquivel-Muelbert et al., 2018; Fadrique et al., 2018; Poloczanska et al., 2013; Scheffers et al., 2016; Steinbauer et al., 2018), critically linking climatological and ecological changes on a system-by-system basis, and attributing them to specific external climate forcing factors, remains challenging. Extending the (palaeo)climatologically concept of DA to ecology is hampered by numerous, often intertwined and nonlinear, system-inherent ecological pathways, factors, processes and feedbacks (i.e. the amplitude of ecological variation independent of climate), as well as the interplay of anthropogenic and natural forcing agents (Parmesan, Duarte, Poloczanska, Richardson, & Singer, 2011; Rosenzweig & Neofotis, 2013). Carefully designed experiments for identifying causal linkages are preferable (Rohr et al., 2011), but often impractical, if the simplicity of their settings lacks the necessary degree of real-world complexity.

In a guidance paper for Lead Authors of the fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC), Hegerl et al. (2010) clarify methods, definitions and terminology of DA related to anthropogenic climate change. Moreover, the authors provide guidelines for good practices in DA studies and their data requirements, and address methods for handling confounding factors. In response to Hegerl et al. (2010) and Parmesan et al. (2011) suggest that extending DA to attribution of biotic responses is ill advised and raise relevant points regarding the difficulty of gaining insights into anthropogenic climate change effects from the response of individual ecosystem components using only DA studies. First, biological reactions are often complex and idiosyncratic, thus, there is a challenge in attributing ecological behaviour to external causes mechanistically. Second, the small sampling sizes of the available ecological datasets make it difficult to detect putative linkages between biotic responses and abiotic drivers, with the later usually operating on much larger scales. Finally, Parmesan et al. (2011) emphasize that DA approaches from climate forcing to climate change and to biological responses, as proposed by Hegerl et al. (2010), are challenged by the fact that there is no common biological response to a single climate driver, and no simple biological metric analogous to global warming.

Excluding system-internal variation and separating ecological effects of anthropogenic climate change from those of natural climate variability would be simpler if biotic responses would be quasilinear. Climatologists could then use DA to estimate the spatial and temporal fingerprint of global warming that is attributable to anthropogenic factors. However, ecological responses are often nonlinear, and sometimes manifest in a threshold-like behaviour known as a tipping point (Burrows et al., 2011; Lenton et al., 2008; Moore, 2018; Rohr et al., 2011; Steffen et al., 2018; Williamson, Bathiany, & Lenton, 2016). Increasing attention is recently being given to the concept of tipping dynamics, which can be equally disruptive for environmental and social systems (Milkoreit et al., 2018; Otto et al., 2020). Ecological tipping points, for instance, are likely to appear when one or several compound climate factors exceed the tolerance range afforded by a species' physiological plasticity, or if the change is too rapid to be compensated by dispersal or genetic adaptation (Breed, Ottewell, Gardner, & Lowe, 2011; Festa-Bianchet & Mysterud, 2018).

Alternatively, species-specific plastic responses could act at the level of the physical environment. Changes in ice cover that result from positive feedback loops have been demonstrated to affect the distributional patterns of Arctic charr *Salvelinus alpinus* L. across Norwegian lakes (Helland, Finstad, Forseth, Hesthagen, & Ugedal, 2011). Moreover, changes in solar radiation, volcanic eruptions and greenhouse gases have caused global warming or cooling in the past. This is the case of natural forcing competing with anthropogenic forcing during the first half of the 20th century (Hegerl, Brönnimann, Schurer, & Cowan, 2018), and being surpassed by it after the 1950s, so that more than half of the temperature change since then can be attributed to human activities (Masson-Delmotte et al., 2013). Anthropogenic forcing, however, consists not only of the radiative effects of greenhouse gases, such as CO₂, CH₄ and N₂O, but also ozone concentrations and aerosols, as well as land-use changes. While all these forcing agents have some global impact, they may exhibit significantly differentiated regional patterns (Cramer et al., 2014). Evidence for spatial heterogeneity in the environmental consequences of climate change is especially strong when considering factors other than temperature. For instance, shifts in the hydrological cycle and associated changes in precipitation and evaporation regimes have implications on salinity and drought patterns, and thus marine and terrestrial habitats (Greve et al., 2014; Hegerl et al., 2015; Kumar et al., 2016; Zhang et al., 2007).

These examples highlight the importance of a mechanistic approach to attribute biotic responses to specific abiotic factors and processes of naturally induced climate variability, with superimposed anthropogenic influences being particularly critical to whether or not the threshold is reached. Coupling of ecological and climatological data, and consideration of the corresponding, cross-disciplinary expertise will afford a more comprehensive understanding of the influences of anthropogenic climate change on externally driven ecosystem behaviour, and provide a framework for quantifying causes and consequences of past, present and future environmental change.

2.2 | Requirements for extending DA to ecology

Linking man-made climate variations to biotic responses with confidence requires particularly large spatiotemporal datasets. While long-term monitoring programmes (e.g. some forest insects, human diseases and game and fish harvests) are still relatively few (Andrew et al., 2017, 2019; Büntgen & Krusic, 2018; Büntgen et al., 2017), alternative datasets may be derived from annually resolved and absolutely dated tree rings, bivalve shells and corals (Büntgen, 2019), as well as other high-resolution proxy archives, including sedimentation records of pollens and micro-organisms (Bradley, 2014; Masson-Delmotte et al., 2013). For example, tree-ring chronologies that extend over hundreds and sometimes thousands of years currently exist for many regions of the extra-tropical landmasses (Esper et al., 2016; St. George, 2014). These records provide evidence of past changes in tree growth (Babst et al., 2019). Moreover, externally driven climate variations that control tree growth can be

detected by combining these data with outputs from climate model simulations (Hegerl et al., 2007), or using mechanistic growth models that may incorporate nonlinear processes in the growth response to climate (Evans, Smerdon, Kaplan, Tolwinski-Ward, & Gonzalez-Rouco, 2014; Sanchez-Salguero et al., 2017). An alternative to continuous long-term monitoring is replicating a historical research project many years after and comparing results (Buckley, Nufio, Kirk, & Kingsolver, 2015). A combination of very long meteorological and ecological observations (i.e. measurements) together with museum and herbarium collections (i.e. proxies) may also provide valuable evidence for global change biology and ecology throughout all seasons (Büntgen et al., 2012; Büntgen & Krusic, 2018).

Studies of ecological responses along environmental gradients have proven useful in understanding anthropogenic effects on biotic systems (Henne et al., 2018). Specifically, when sufficiently long records are lacking, spatially extensive data may provide additional degrees of freedom, thus acting as a surrogate for time. The potentials and limitations of space-for-time substitution studies relevant to climate change research (Johnson & Miyanishi, 2008), however, often remain debatable (Fukami & Wardle, 2005), because of incomplete knowledge of land-use/land-cover histories. Responses to anthropogenic climate change may also be slower than space-for-time substitutions would predict, owing to ecological time lags, dispersal limitations and/or adaptation rates (Fukami & Wardle, 2005). These caveats notwithstanding, space-for-time substitutions can provide promising data for a DA approach to link anthropogenic climate change to biotic dynamics. The increased availability and quality of satellite imagery and remote sensing in ecology, for instance, offer new data sources for space-for-time studies (Davies & Asner, 2014; Kays, Crofoot, Jetz, & Wikelski, 2015; Peura et al., 2016; Vierling, Vierling, Gould, Martinuzzi, & Clawges, 2008).

Inference-based simulation modelling is a powerful method for attributing variability to multiple external drivers in nonlinear systems (Ionides, Breto, & King, 2006; Wassmann & Lenton, 2012; Williamson et al., 2016). Models for DA of biotic responses will preferably contain two sequential responses: (a) climatic responses to external drivers and (b) ecological responses to external drivers and/or resulting climatic fluctuations. The first step is to use a classic DA analysis, where climatologists quantify covariance between climate fluctuations and multiple external forcing agents to attribute variance to the different drivers (Christidis et al., 2012; Hegerl et al., 2010). This method can be used to simulate climate variables under different potential forcing scenarios that are relevant for the functioning and productivity of ecological systems (Cramer et al., 2014). In parallel, environmental time series and other context type information of biotic systems can be used to build ecological response models, which are standard impact-oriented models (Johnson et al., 2010). This can be done by using a statistical downscaling model to estimate the effect of climate variables on ecological changes using previously calibrated relationships with independent data (Marini et al., 2017).

Alternatively, climate effects can be quantified using a forward model that physically describes the processes through which climate

influences the ecological variables (Anchukaitis et al., 2006; Johnson et al., 2010; Sanchez-Salguero et al., 2017; Shishov et al., 2016). By incorporating nonlinear relationships, both methods allow for estimating uncertainties by changing either parameters in the climate-ecological model or the climate information that feeds directly into the ecological model. Both approaches can also incorporate the evaluation of climate response signatures in the context of past and/or future climate change. A control run produced with constant pre-industrial forcing specifications (piControl; Taylor, Stouffer, & Meehl, 2012) can represent internal climate variability as a reference for non-perturbed climate conditions. If the aim is to consider the relative effects of natural versus anthropogenic forcing within the historical period or the last millennium, groups of natural-only or anthropogenic-only forcing responses can be considered to compare with the evolution of the climate variables during a certain period of time (Duan et al., 2019; Hegerl et al., 2010, 2011; Masson-Delmotte et al., 2013; Melo-Aguilar, González-Rouco, García-Bustamante, Navarro-Montesinos, & Steinert, 2018; Schurer et al., 2013, 2014, 2019; Wang et al., 2018); ensembles of simulations incorporating all possible forcing agents or specific simulations addressing a single forcing are also typically considered (Otto-Bliesner et al., 2016). Alternatively, if observations have to be compared for consistency against potential future climate change states, different scenarios of future forcing changes (Taylor et al., 2012) can be considered. Using outputs from different simulations with different models under several forcing scenarios and starting from different initial conditions, allows for quantification of uncertainties related to different forcing pathways, model physics and internal variability in the Earth's climate system. The ecological response can be quantified from such simulations using results from downscaling or forward modelling compared to empirical ecological data to identify which climate forcing group or scenario best fits the observed patterns.

2.3 | The larch budmoth system

The LBM (*Z. diniana* or *griseana* Gn.) is a native forest pest of subalpine larch forests that has historically caused forest defoliation predominantly between around 500 and 2,000 m elevation in the European Alps (Baltensweiler & Rubli, 1999). LBM population densities have fluctuated between ~1 and 20,000 larvae per host tree (*Larix decidua* Mill.) on an 8- to 9-year cycle (Büntgen et al., 2009; Esper, Büntgen, Frank, Nievergelt, & Liebhold, 2007; Saulnier et al., 2017), resulting in periodic defoliation of large tracts of forest at peak densities (Turchin et al., 2003). The LBM outbreak events have been shown to decrease biomass accumulation of the host forests (Peters, Klesse, Fonti, & Frank, 2017). LBM defoliation events can be detected in the annual rings of their larch host trees (Büntgen, Liebhold, et al., 2020; Rolland, Baltensweiler, & Petitcolas, 2001), providing a window into past LBM outbreak patterns. Two important patterns have been revealed in the analysis of LBM outbreaks in the Alps. Firstly, the persistency of regular LBM outbreak cycles over, at least, the past 1,200 years in the Lötschental valley of the western Swiss Alps (Esper et al., 2007).

Secondly, a weakening of the intensity of regular outbreaks from the early 1980s onwards (Baltensweiler, 1993), which corresponds with a European-wide temperature increase (Büntgen et al., 2011; Büntgen, Liebhold, et al., 2020). The ecophysiological mechanism(s) of LBM population dynamics are, however, still not fully resolved. An Alpine-wide network of 65 larch chronologies further suggests changes in winter temperature over the last 200 years caused elevational outbreak shifts and LBM cycle destabilization in the late 20th century. Johnson et al. (2010) used a population model to show that that winter warming over the 20th century may have caused upward elevational range shifts in LBM outbreaks. The upward shift to near or above the upper tree line ecotone in the European Alps (Moser et al., 2010) would reduce resources available to the moth and suppress population peak densities (Battipaglia et al., 2014; Büntgen, Liebhold, et al., 2020; Hartl-Meier et al., 2017; Konter et al., 2015).

Here we use the LBM system as an ecological case study to introduce a method for assessing the possible attribution of anthropogenic climate change, as opposed to natural climate variability, to the upward elevational shift and reduction in peak densities of LBM population cycles (Figure 1). Our example from the Swiss Alps is particularly timely since it provided a millennium-long context for the substantial recent winter warming that shifts late-20th century LBM

outbreak epicentres upward in elevation to near or above the upper tree line ecotone where resource availability to the moth is reduced.

2.4 | From 'Detection' to 'Attribution'

To extend the above study beyond 'Detection' to 'Attribution', we assess the elevational dynamics of LBM outbreaks on simulated Alpine winter temperature fluctuations from 'The Community Earth System Model-Last Millennium Ensemble' (CESM-LME; Otto-Bliesner et al., 2016). Using $\sim 2^\circ$ resolution in the atmosphere and land components, CESM-LME expands on the CMIP5 and earlier LM model simulations by providing the largest ensemble of last millennium simulations with a single model to date. The CESM-LME uses the CMIP5 climate forcing reconstructions (Schmidt et al., 2011) and contains both 'full forcing' simulations containing all last millennium forcing agents, as well as ensembles of simulations with each forcing individually (greenhouse gases, ozone and aerosols, land-use, volcanic eruptions, solar variability, orbital changes). In using the most recent version of the comprehensive CESM (Hurrell et al., 2013), the herein employed state-of-the-art multi-model climate ensemble approach adds understanding into the role of internal variability versus

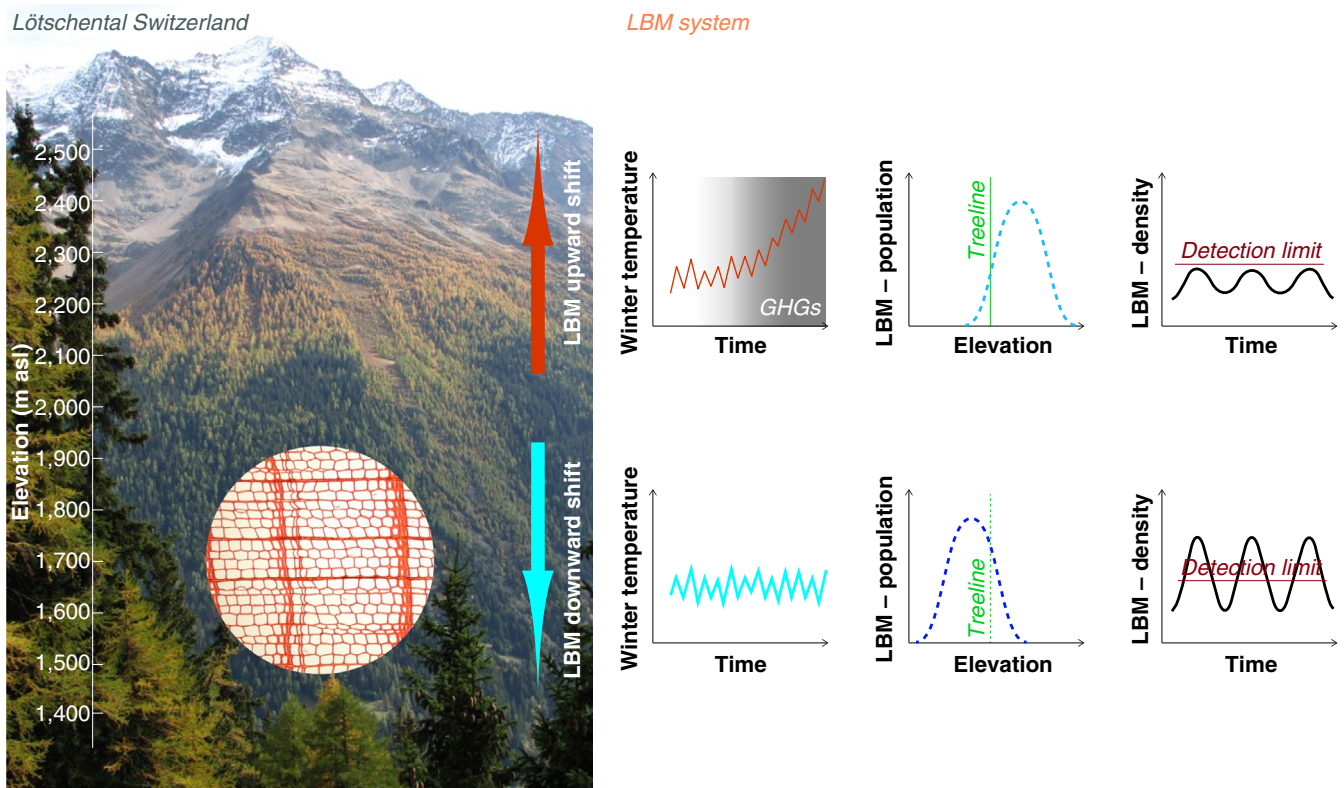


FIGURE 1 South-exposed slope of the Lötschental (c. $46^\circ 29'N$ and $8^\circ 17'E$), the largest northern side valley of the Rhone valley in the western Swiss Alps (Büntgen, Frank, Nievergelt, & Esper, 2006), where cyclic population outbreaks of the larch budmoth (LBM; *Zeiraphera diniana* or *griseana* Gn.) defoliate the subalpine larch forest every 8–9 years (Esper et al., 2007), and leave distinct growth depressions in the host's tree rings (inset circle; Büntgen et al., 2009). Anthropogenic winter warming causes substantial upward elevational range shifts in LBM outbreak epicentres that suppress the insect's population peak density below a certain detection threshold (upper sketch line). No such effects occur under stable temperatures without greenhouse gas or other external forcing, because the LBM system is best known for its persistent regular behaviour (lower sketch line)

external forcing in generating climate variations over the last 12 centuries (Otto-Bliesner et al., 2016). Annual winter temperatures of the monthly means from December to February and averaged from 12 grid points over the Alpine arc (6–16°E and 44–48°N) were extracted from control and forced model runs. With the exception of combined ozone and aerosol simulations (1851/52–2004/5 CE), all other model output reaches back to the winter 851/52 CE. The climate simulations were coupled with a spatial model of LBM population dynamics (Johnson et al., 2010), in which population growth rates were a function of winter temperatures.

The effects of anthropogenic climatic forcing on LBM population dynamics were explored by a discrete time tri-trophic model where the insect's pre-dispersal population dynamics are coupled with pre-dispersal population dynamics of parasitoids and the quality of the larch host tree foliage. LBM population dynamics are most consistent with regulation by both parasitoids and host needle quality (Baltensweiler & Rubli, 1999). Parameter values were empirically derived and the model was selected based on the best fit to empirical population dynamics of LBM (Turchin et al., 2003). The model was spatially extended by linking multiple populations with moth and parasitoid dispersal using exponential dispersal kernels. This model has been used to capture the recurrent west–east travelling waves of LBM outbreaks across the Alpine arc in the mid- to late-20th century (Johnson, Bjørnstad, & Liebhold, 2004). The method was used later to demonstrate that the travelling LBM outbreak waves vary along an elevational gradient, and that the elevation of the outbreak epicentre is affected by winter temperatures (Johnson et al., 2010). Previous studies have shown that elevation has a unimodal impact on the growth rates of LBM populations (Baltensweiler & Rubli, 1999). The spatially extended population model suggests that outbreak epicentres occur at or near elevations where the LBM growth rate is greatest (Johnson et al., 2010).

In this study, we use the relationship between growth rate and elevation estimated by Johnson et al. (2010), and link the temperature component of the population model to the simulated temperature anomalies. From the simulations, we calculate epicentre elevations using wavelet phase analysis (Grenfell, Bjørnstad, & Kappey, 2001). Phase angle values range from -180° to 180° . As a population cycles from a trough to a peak, the phase angle

increases from -180° to 0° . As a population cycles from a peak to a trough, the phase angle continues to increase from 0° to 180° (Johnson et al., 2004). In this study, the elevation with the largest phase angle is identified as the location of the travelling wave epicentre. The magnitudes of LBM population cycles are estimated by identifying the maximum population density over 10-year intervals, which approximates the typical 8- to 9-year length of LBM cycles (Turchin et al., 2003). The population dynamics are simulated across a potential elevational range from 400 to 2,200 m a.s.l. The one-dimensional gradient is separated into 181 locations at 10-m intervals. Dispersal across elevation is modelled with isotropic movement. The effects of different climatic forcing agents on the elevation of epicentre and magnitude of cycles are explored by simulating LBM population dynamics under each scenario. In each simulation, LBM population dynamics are coupled with winter temperature anomalies from the respective forcing scenario. Epicentre elevations are estimated from the simulated LBM population dynamics using wavelet and phase angle analysis (Johnson et al., 2004). Model performance is assessed by comparing the likelihoods that empirical phase angle–elevation relationships (Johnson et al., 2010) would be produced by the population model under each of the various climate forcing scenarios. All analyses are performed in Matlab R2012b (see Johnson et al., 2004, 2010 for methodological details). Supplementary to the above, we refer to Otto-Bliesner et al. (2016) and Johnson et al. (2004, 2010) for gaining further insights into 'The Community Earth System Model-Last Millennium Ensemble' (CESM-LME) modelling project and the ecological LBM model respectively.

3 | RESULTS

The modelled mean Alpine December–February temperature anomalies using a single control run and 10 different simulations with all forcing agents are summarized in Figure 2, whereas the six scenario simulations each with a single forcing factor are provided in Figure 3. In the forced scenario including anthropogenic CO_2 , CH_4 , and N_2O increase, a pronounced nonlinear rise in Alpine winter temperatures is simulated in the late 20th century. Comparison of the all

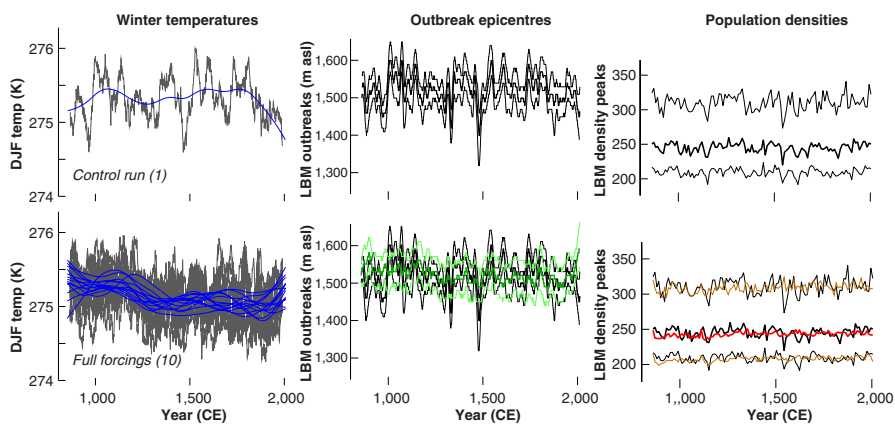


FIGURE 2 Control run and the fully forced simulations of December–February temperature means over the European Alps (blue lines are 30-year splines; left). Elevational changes in larch budmoth (LBM) outbreak epicentres (mean ± 1 SD) under the different climate simulations (middle), and the corresponding LBM population densities at cycle peaks (mean ± 1 SD; right). Outbreak epicentre and density peaks for full forcing simulations (green) are overlaid on those from control simulations (black) for comparison (bottom row, middle and right)

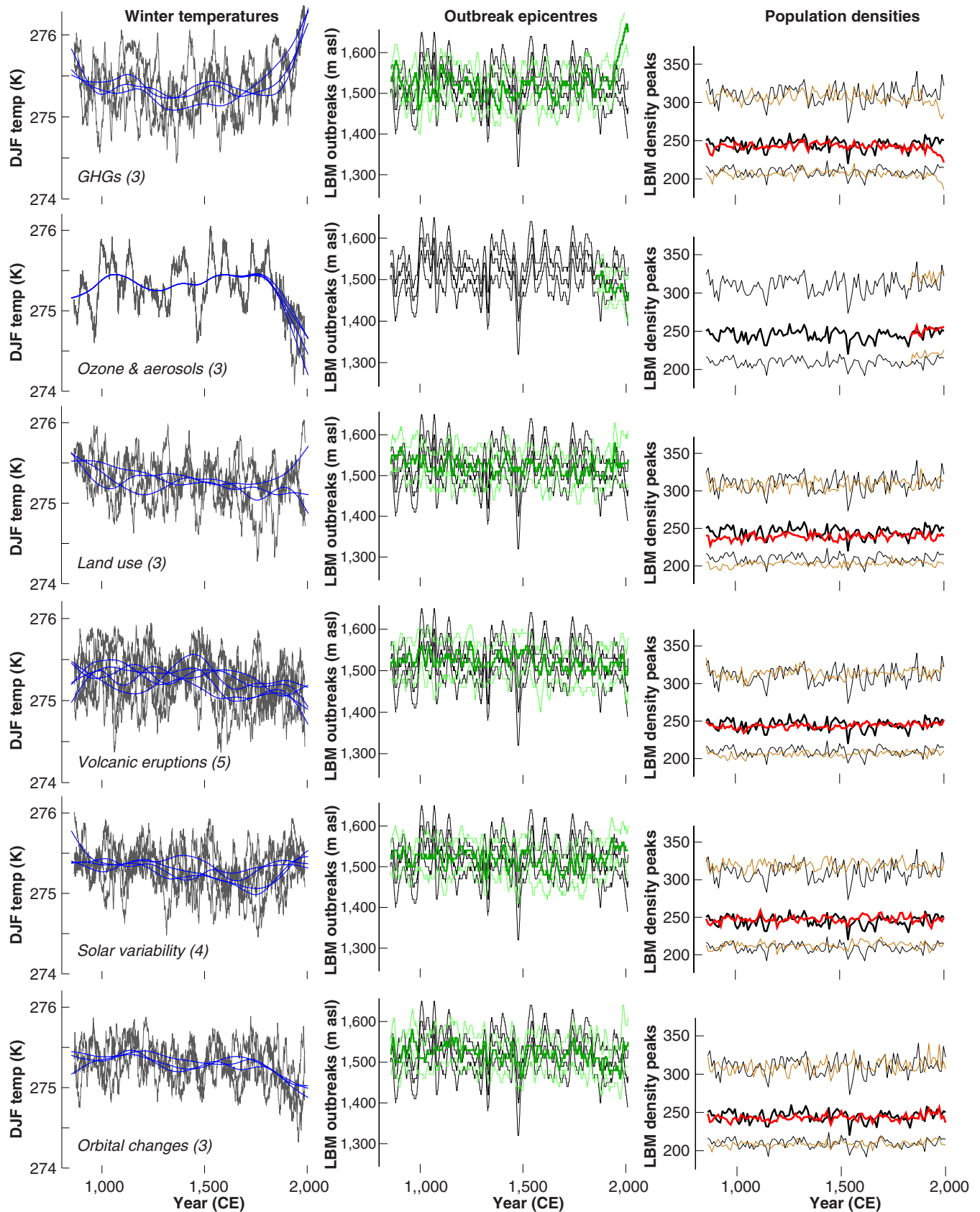


FIGURE 3 Single forcing simulations of Alpine winter temperatures (blue lines are 30-year splines; left). Elevational changes in larch budmoth (LBM) outbreak epicentres under different climate simulations (mean \pm 1 SD; middle), and corresponding LBM population densities at cycle peaks (mean \pm 1 SD; right). Outbreak density peaks for single forcing simulations (green, red) are overlaid on control simulations (black). Ozone and aerosol runs are reliable after 1850 CE

forcing simulations (Figure 2) with the single forcing sub-ensembles (Figure 3) suggests that the increase in greenhouse gases is the primary driver of the 20th century elevation increase in the full forcing scenario (Figures 2 and 3). In contrast, aerosol forcing, volcanic activity and orbital changes would contribute to a clear decline in 20th century temperatures, and thus to a less pronounced winter temperature increase in the 20th century. Solar forcing causes a small 20th century temperature increase, and land-use changes trigger a multi-centennial cooling that ends in a lack of agreement during the 20th century with one (two) simulation rendering temperature increase (decrease).

The results of the simulations with all climate forcing factors and those with greenhouse gas forcing simulate an increase in the epicentre elevation from the year 1860–2000 CE (Figures 2 and 3), which is qualitatively consistent with empirical observations of LBM population dynamics in the European Alps over the last 150 years (Johnson et al., 2010). Model fit analyses suggest that the simulations with all forcing factors have strong support over the other single forcing experiments, which had Δ log-likelihoods from 16.9 to 55.3 (Table 1). The control run with no forcing ranked seventh out of the eight models with a Δ log-likelihood of 33.0, thus indicating the importance of external forcing factors for ecological system behaviour.

By assuming stability of the ecological system and by coupling the LBM tri-trophic model with the winter temperature anomalies, we are able to explain changes in elevational LBM outbreak dynamics in relationship to internal variability and external climate forcing. Epicentre elevations generated by the control simulation are provided in Table 2. Epicentre elevations simulated by the experiments with external forcing are overlaid on those generated from the control run for comparison (Figure 2). The simulations with all forcing factors and with greenhouse gas forcing only produce outbreak epicentre increases of 59 and 148 m, respectively, in the 20th century (Table 2). In contrast, the forced ensemble using

TABLE 1 Fits of the empirical data represented in elevation-phase angle relationships from fig. 2a in Johnson et al. (2010) to simulated data from the control and seven forcing scenarios. All phase angles are normalized to mean = 0 and unit variance prior to $-\log$ likelihood estimation. A lower $-\log$ likelihood indicates a better fit. Δ log likelihood is difference between the respective model and the best fit model

Forcing factors	$-\log$ likelihood	Δ log likelihood
All forcing	345.8	0
Ozone and aerosols	362.7	16.9
Land use	363.9	18.1
Volcanic eruptions	367.0	21.2
Greenhouse gases	367.9	22.1
Orbital changes	375.5	29.7
Control run	378.8	33.0
Solar variability	401.1	55.3

TABLE 2 Model predictions for the change in larch budmoth epicentre elevation and peak population densities by comparing the average epicentre elevations and peak population densities from 1995 to 2005 CE to the historical estimates. Median (25% and 75% quantiles) change in elevation is estimated for epicentre elevation because of non-normality of the epicentre data. Mean (\pm SD) peak densities are percentage changes from historical estimates. Historical simulation estimates are calculated from 851 to 1850 CE

Forcing factors	Δ epicentre elevation [25th, 75th quartile]	% Δ peak density [\pm 1 SD]
Control run	-72 [-111, -29] m	2 [-26 17]%
All forcing	59 [16,105] m	0 [-26 14]%
Greenhouse gas	148 [104, 197] m	-9 [-34 5]%
Ozone and aerosols	-73 [-113, -30] m	6 [-34 5]%
Volcanic eruptions	-33 [-78, 15] m	2 [-24 18]%
Land use	12 [-30, 58] m	0 [-27 15]%
Orbital changes	7 [-35, 52] m	-1 [-28 14]%
Solar variability	36 [-9, 86] m	3 [-26 17]%

ozone and aerosols simulates a decrease in the epicentre elevation by 73 m during the increase in anthropogenic aerosols (Figure 3), which contribute to dampening and delay the observed increase, as it happens with temperatures (Hegerl et al., 2010). The experiments that consider volcanic eruptions, land-use, orbital changes and solar variability had minor effects on the predicted insect outbreak epicentres of 36 m or less, which do not stand out of the long-term variability of this parameter. These results suggest that the 20th century increase in LBM outbreak epicentres can be primarily attributed to an increase in greenhouse gases, and also the aerosol forcing translates into a lower and somehow delayed increase. The LBM population peak densities in the seven external forcing scenarios show no divergence from those generated by the control model with the exception of the greenhouse gas scenario (Figure 3). While a dampening of LBM population cycles under future warming was predicted by Johnson et al. (2010), this is a weak trend that is within one standard deviation of the time series. Moreover, a reduction of population cycles is not detected in the fully forced scenarios.

Our results support the hypothesis that anthropogenic warming due to greenhouse gases is the primary cause of detectable changes in spatial population dynamics of the LBM in the European Alps (Johnson et al., 2010). Specifically, in the model simulations with natural and anthropogenic forcing agents, the epicentre of travelling LBM waves shifted upward by an estimated 59 m in elevation. The effects of increasing 20th century greenhouse gases alone are estimated to be a 148 m upward elevational shift in LBM outbreak epicentre. Note that other possible effects on LBM population dynamics, such as increased nitrogen deposition rates and modified forest management strategies, are not considered. Notably, a reduction in the larch forest cover has been linked to the decline in detectable LBM outbreaks in recent years (Battipaglia et al., 2014; Hartl-Meier et al., 2017).

4 | DISCUSSION

The routine implementation of DA into ecological research depends on the ability to unravel the causes and consequences of recent biotic changes. Introducing ongoing ecological changes against the backdrop of natural and anthropogenic climate change and tracking historical analogues, however, requires large spatially and temporally resolved data, as well as an understanding of internal ecological variability that may or may not occur independent of climate or any other external forcing. Improved monitoring efforts and high spatiotemporally resolved proxy archives are required for assessing the effects of both, extreme climatic events and long-term trends in climatic means, on tipping points and collapses in biological and ecological, as well as social systems. Moreover, anthropogenic emissions can cause dangerous tipping points in the Earth's climate system itself. In addition, climate model outputs need to distinguish anthropogenic from natural external forcing, and those from internal climate variability. Interdisciplinary science is overcoming the methodological and technological barriers to detect and separate external climatic drivers of ecological responses only if internal system variability is known. This is becoming possible by the ability of high-resolution climate proxy reconstructions and state-of-the-art climate model simulations to place modern environmental conditions in a long-term context. Moreover, new Earth System Models become available that integrate the interactions of atmosphere, ocean, land, ice and biosphere to estimate the state of regional and global climate under a wide variety of conditions. Earth System Models open the possibility to have the following: progressively higher spatial resolution; an increased number of processes and the level of physical complexity, which allows for the inclusion of more complex model components, dynamical vegetation modules or biogeochemical cycles; and ensembles of simulations of future and past forcing scenarios instead of single model experiments. Longer and higher resolved simulations can now be created in shorter time spans, and together with proxy archives this will facilitate a better understanding of the relative effects of human action on biotic systems, and thus provide insight for management strategies. We therefore suggest an application of DA at the interface of ecology and climatology that considers complex processes and interacting effects within and between the Earth's biotic and climatic systems.

Existing barriers to identification of causal linkages between climatology and ecology can be overcome through interdisciplinary collaboration and the use of inference-based model analysis. Moreover, organismal and population ecologists can learn from current ecosystem-level climate change research. Ecosystem responses are related to climatic changes by either experimental manipulation of environmental variables or rigorous evaluation of covariance in climatic and ecological datasets. Most experiments involve laboratory-based manipulations of environmental factors such as temperature and CO₂, and measured organismal responses. However, some large-scale experiments in real world environments have been successful. For example, the Free Air

Carbon Enrichment project takes the experimental approach to understand ecosystem responses to climate fluctuations in a forest environment, but also to linking ecosystem processes to patterns at the community, population and organismal levels (Andresen et al., 2018; Mohan et al., 2006; Obermeier, Lehnert, Ivanov, Luterbacher, & Bendix, 2018; Obermeier et al., 2017; Yuan et al., 2018). These experimental approaches to global change biology allow identification of underlying mechanistic relationships that impact ecological systems, but generally lack the ability to attribute responses to particular climatic drivers. Projects that analyse the relationship between microclimatic fluctuations and ecological reactions, such as FLUXNET, a global network of more than 500 micrometeorological tower sites across five continents that use eddy covariance methods to measure the exchanges of carbon dioxide, water vapour and energy between terrestrial ecosystems and the atmosphere (Wolf, Field, & Berry, 2011), may be appropriate for extending DA to ecology.

Collaborations in an interdisciplinary research arena should include key components from the interacting intellectual and methodological silos to test strong inferences with rigorous model validation. DA may also be opportune at the forefront of other research fields, such as climate change and disease investigation (Lafferty, 2009; Rohr et al., 2011). Estimation of the phylogenetic diversity of species and their reductions in body size under future climate change (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011; Thuiller et al., 2011) may also benefit from DA. Historical and epidemiological signs of relationships between hydroclimatic swings and plague outbreaks in medieval Europe (Büntgen et al., 2011; Ljungqvist et al., 2018; Schmid et al., 2015), long before we started altering the Earth's atmospheric composition substantially, is one of numerous palaeoclimatic challenges that would benefit from broadening DA to investigate the impacts of natural external forcing factors. Even more exciting could be a linkage between the evolution of ancient societies and environmental variations as far back as the Neolithic Revolution ~7,500 years ago when Europe's climate became warmer (Tegel, Hinkel, & Büntgen, 2012).

5 | CONCLUSIONS

After reviewing recent developments in DA research, we use the LBM system as an example to expand the climatological concept of DA to global change ecology. We show that anthropogenic warming shifts the epicentre of travelling LBM waves upward, and thus disrupts the intensity of cyclic population outbreaks that persisted over the past 1,000 years in the European Alps. This finding describes the ability to detect ecological responses beyond internal system variability, to attribute them to a specific climate forcing factors, and to identify ecological tipping points in a warming world.

Moreover, our LBM case study emphasizes four key points associated with the conceptual extension of DA to both, theoretical and

applied, biological and ecological research: (a) Ensembles of climate simulations with a separation of forcing factors provide a new and powerful tool to better understand the role of humans in shaping environmental systems; (b) ecological studies are now able to better separate the effects of natural from anthropogenic climate change; (c) climate reconstructions and model simulations shall routinely inform inference-based ecological modelling to identify the causal effects of different climatic drivers; and (d) improved understanding of global change ecology will ultimately better guide ecosystem management and environmental policy at local to global scales.

ACKNOWLEDGEMENTS

U.B. received funding from the SustES Project (CZ.02.1.01/0.0/0.0/16_019/0000797). J.F.G.-R. acknowledges the projects ILMoelS_CGL2014-59644-R and GReatMoelS_RT1218-102305-B-C21. J.L. is thankful to the JPI-Climate/Belmont Forum collaborative Research Action 'INTEGRATE', and the Climate Science for Service Partnership China project (CSSP China).

AUTHORS' CONTRIBUTIONS

U.B. and D.M.J. designed the study and wrote the paper with input from J.F.G.-R., J.L. and N.C.S.; D.M.J. performed the analyses and J.F.G.-R. provided model data. All authors provided conceptual and methodological input, and contributed with critical discussion.

DATA AVAILABILITY STATEMENT

All data and codes supporting this article are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.b5mkkwh9x> (Büntgen, González-Rouco, Luterbacher, Stenseth, & Johnson, 2020).

ORCID

Ulf Büntgen  <https://orcid.org/0000-0002-3821-0818>

REFERENCES

- Anchukaitis, K. J., Evans, M. N., Kaplan, A., Vaganov, E. A., Hughes, M. K., Grissino-Mayer, H. D., & Cane, M. A. (2006). Forward modeling of regional scale tree-ring patterns in the southeastern United States and the recent influence of summer drought. *Geophysical Research Letters*, 33. <https://doi.org/10.1029/2005GL025050>
- Andresen, L. C., Yuan, N., Kammann, C., Seibert, R., Moser, G., Grünhage, L., ... Müller, C. (2018). Biomass responses in a temperate European grassland through 17 years of elevated CO₂. *Global Change Biology*, 24, 3875–3885.
- Andrew, C., Büntgen, U., Egli, S., Senn-Irlet, B., Grytnes, J.-A., Heilmann-Clausen, J., ... Kauseud, H. (2019). Open-source data reveal how collections-based fungal diversity is sensitive to global change. *Applications in Plant Sciences*, 7, e1227. <https://doi.org/10.1002/aps3.1227>
- Andrew, C., Heegaard, E., Kirk, P., Bässler, C., Heilmann-Clausen, J., Krisai-Greilhuber, I., ... Kauseud, H. (2017). Big data integration: Pan-European fungal species observations' assembly for addressing contemporary questions in ecology and global change biology. *Fungal Biology Reviews*, 31, 88–98. <https://doi.org/10.1016/j.fbr.2017.01.001>
- Babst, F., Boiriaux, O., Poulter, B., Trouet, V., Girardin, M. P., & Frank, D. C. (2019). Twentieth century redistribution in climatic drivers of global tree growth. *Science Advances*, 5, eaat4313. <https://doi.org/10.1126/sciadv.aat4313>
- Baltensweiler, W. (1993). Why the larch bud moth cycle collapsed in the subalpine larch-cembra pine forests in the year 1990 for the first time since 1850. *Oecologia*, 94, 62–66. <https://doi.org/10.1007/BF00317302>
- Baltensweiler, W., & Rubli, D. (1999). Dispersal: An important driving force of the cyclic population dynamics of the larch bud moth, *Zeirapera diniana* Gn. *Forest Snow and Landscape Research*, 74, 1–153.
- Barnett, T. P., Hasselmann, K., Chelliah, M., Delworth, T., Hegerl, G., Jones, P., ... Tett, S. (1999). Detection and attribution of recent climate change: A status report. *Bulletin of the American Meteorological Society*, 80, 2631–2659. [https://doi.org/10.1175/1520-0477\(1999\)080<2631:DAAORC>2.0.CO;2](https://doi.org/10.1175/1520-0477(1999)080<2631:DAAORC>2.0.CO;2)
- Barnett, T. P., Pierce, D. W., & Schnur, R. (2001). Detection of anthropogenic climate change in the world's oceans. *Science*, 292, 270–274. <https://doi.org/10.1126/science.1058304>
- Battipaglia, G., Büntgen, U., McCloskey, S., Blarquez, O., Denis, N., Paradis, L., ... Carcaillet, C. (2014). Long-term effects of climate and land-use change on larch budmoth outbreaks in the French Alps. *Climatic Research*, 62, 1–14. <https://doi.org/10.3354/cr01251>
- Bindoff, N. L., Stott, P. A., AchutaRao, K. M., Allen, M. R., Gillett, N., Gutzler, D., ... Zhang, X. (2013). Detection and attribution of climate change: From global to regional. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the fifth assessment report of the Intergovernmental Panel on Climate Change* (pp. 867–952). Cambridge, UK and New York, NY: Cambridge University Press.
- Bradley, R. S. (2014). *Paleoclimatology: Reconstructing climates of the quaternary* (3rd ed., p. 675). San Diego, CA: Elsevier/Academic Press.
- Breed, M. F., Ottewill, K. M., Gardner, M. G., & Lowe, A. J. (2011). Clarifying climate change adaptation responses for scattered trees in modified landscapes. *Journal of Applied Ecology*, 48, 637–641. <https://doi.org/10.1111/j.1365-2664.2011.01969.x>
- Buckley, L. B., Nufio, C. R., Kirk, E. M., & Kingsolver, J. G. (2015). Elevational differences in developmental plasticity determine phenological responses of grasshoppers to recent climate warming. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150441. <https://doi.org/10.1098/rspb.2015.0441>
- Büntgen, U. (2019). Re-thinking the boundaries of dendrochronology. *Dendrochronologia*, 53, 1–4. <https://doi.org/10.1016/j.dendro.2018.10.012>
- Büntgen, U., Frank, D. C., Liebhold, A., Johnson, D., Career, M., Urbinati, C., ... Esper, J. (2009). Three centuries of insect outbreaks across the European Alps. *New Phytologist*, 182, 929–941. <https://doi.org/10.1111/j.1469-8137.2009.02825.x>
- Büntgen, U., Frank, D. C., Nievergelt, D., & Esper, J. (2006). Summer temperature variations in the European Alps, AD 755–2004. *Journal of Climate*, 19(2), 5606–5623. <https://doi.org/10.1175/JCLI3917.1>
- Büntgen, U., González-Rouco, J. F., Luterbacher, J., Stenseth, N. C., & Johnson, D. M. (2020). Data from: Extending the climatological concept of 'Detection and Attribution' to global change ecology in the Anthropocene, v2. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.b5mkkwh9x>
- Büntgen, U., Greuter, L., Bollmann, K., Jenny, H., Liebhold, A., Galvan, J. D., ... Mysterud, A. (2017). Elevational range shifts in four mountain ungulate species from the Swiss Alps. *Ecosphere*, 8, e01761. <https://doi.org/10.1002/ecs2.1761>
- Büntgen, U., Kauseud, H., & Egli, S. (2012). Linking mushroom productivity and phenology to climate variability. *Frontiers in Ecology and the Environment*, 10, 14–19. <https://doi.org/10.1890/110064>
- Büntgen, U., & Krusic, P. J. (2018). Non-traditional data and innovative methods for autumn climate change ecology. *Climatic Research*, 75, 215–220.
- Büntgen, U., Liebhold, A., Nievergelt, D., Wermelinger, B., Roques, A., Reinig, F., ... Esper, J. (2020). Return of the moth: Rethinking the

- effect of climate on insect outbreaks. *Oecologia*, 192, 543–552. <https://doi.org/10.1007/s00442-019-04585-9>
- Büntgen, U., Tegel, W., Nicolussi, K., McCormick, M., Frank, D., Trouet, V., ... Esper, J. (2011). 2500 years of European climate variability and human susceptibility. *Science*, 331, 578–582. <https://doi.org/10.1126/science.1197175>
- Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M., ... Richardson, A. J. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science*, 334, 652–655. <https://doi.org/10.1126/science.1210288>
- Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026. <https://doi.org/10.1126/science.1206432>
- Christidis, N., Stott, P. A., Jones, G. S., Shiogama, H., Nozawa, T., & Luterbacher, J. (2012). Human activity and warm seasons in Europe. *International Journal of Climatology*, 32, 225–239. <https://doi.org/10.1002/joc.2262>
- Cramer, W., Yohe, G. W., Auffhammer, M., Huggel, C., Molau, U., da Silva Dias, M. A. F., ... Tibig, L. (2014). Detection and attribution of observed impacts. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the fifth assessment report of the Intergovernmental Panel on Climate Change* (pp. 979–1037). Cambridge, UK and New York, NY: Cambridge University Press.
- Davies, A. B., & Asner, G. P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology & Evolution*, 29, 681–691. <https://doi.org/10.1016/j.tree.2014.10.005>
- Duan, J., Ma, Z., Wu, P., Xoplaki, E., Hegerl, G., Li, L., ... Luterbacher, J. (2019). Detection of human influences on temperature seasonality from the 19th century. *Nature Sustainability*, 2, 484–490. <https://doi.org/10.1038/s41893-019-0276-4>
- Esper, J., Büntgen, U., Frank, D. C., Nievergelt, D., & Liebhold, A. (2007). 1200 years of regular outbreaks in alpine insects. *Proceedings of the Royal Society B: Biological Sciences*, 274, 671–679. <https://doi.org/10.1098/rspb.2006.0191>
- Esper, J., Krusic, P. J., Ljungqvist, F. C., Luterbacher, J., Carrer, M., Cook, E., ... Büntgen, U. (2016). Ranking of tree-ring based temperature reconstructions of the past millennium. *Quaternary Science Reviews*, 145, 134–151. <https://doi.org/10.1016/j.quascirev.2016.05.009>
- Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J., Feldpausch, T. R., ... Higuchi, N. (2018). Compositional response of Amazon forests to climate change. *Global Change Biology*, 25, 39–56.
- Evans, M. N., Smerdon, J. E., Kaplan, A., Tolwinski-Ward, S. E., & Gonzalez-Rouco, J. F. (2014). Climate field reconstruction uncertainty arising from multivariate and nonlinear properties of predictors. *Geophysical Research Letters*, 41, 9127–9134. <https://doi.org/10.1002/2014GL02063>
- Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., ... Feeley, K. J. (2018). Widespread but heterogeneous responses of Andean forests to climate change. *Nature*, 564, 207–212. <https://doi.org/10.1038/s41586-018-0715-9>
- Feder, M. E. (2010). Physiology and global climate change. *Annual Reviews of Physiology*, 72, 123–125. <https://doi.org/10.1146/annurev-physiol-091809-100229>
- Festa-Bianchet, M., & Mysterud, A. (2018). Hunting and evolution: Theory, evidence, and unknowns. *Journal of Mammalogy*, 99, 1281–1292. <https://doi.org/10.1093/jmammal/gyy138>
- Fukami, T., & Wardle, D. A. (2005). Long-term ecological dynamics: Reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2105–2115. <https://doi.org/10.1098/rspb.2005.3277>
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, 26, 285–291. <https://doi.org/10.1016/j.tree.2011.03.005>
- Grenfell, B. T., Björnstad, O. N., & Kappey, J. (2001). Travelling waves and spatial hierarchies in measles epidemics. *Nature*, 414, 716–723. <https://doi.org/10.1038/414716a>
- Greve, P., Orowsly, B., Mueller, B., Sheffield, J., Reichstein, M., & Seneviratne, S. I. (2014). Global assessment of trends in wetting and drying over land. *Nature Geosciences*, 7, 716–721. <https://doi.org/10.1038/ngeo2247>
- Hartl-Meier, C., Esper, J., Liebhold, A., Konter, O., Rothe, A., & Büntgen, U. (2017). Effects of host abundance on larch budmoth outbreaks in the European Alps. *Agricultural and Forest Entomology*, 19, 376–387. <https://doi.org/10.1111/afe.12216>
- Hasselmann, K. (1993). Optimal fingerprints for the detection of time-dependent climate change. *Journal of Climate*, 6, 1957–1971. [https://doi.org/10.1175/1520-0442\(1993\)006<1957:OFFTDO>2.0.CO;2](https://doi.org/10.1175/1520-0442(1993)006<1957:OFFTDO>2.0.CO;2)
- Hegerl, G. C., Black, E., Allan, R. P., Ingram, W. J., Polson, D., Trenberth, K. E., ... Zhang, X. (2015). Challenges in quantifying changes in the global water cycle. *Bulletin of the American Meteorological Society*, 96, 1097–1115. <https://doi.org/10.1175/BAMS-D-13-00212.1>
- Hegerl, G. C., Brönnimann, S., Schurer, A., & Cowan, T. (2018). The early 20th century warming: Anomalies, causes, and consequences. *WIREs Climate Change*, 9, e522. <https://doi.org/10.1002/wcc.522>
- Hegerl, G. C., Crowley, T., Allen, M., Hyde, W. T., Pollack, H., Smerdon, J., & Zorita, E. (2007). Detection of human influence on a new 1500-year climate reconstruction. *Journal of Climate*, 20, 650–666. <https://doi.org/10.1175/jcli4011.1>
- Hegerl, G. C., Crowley, T., Hyde, W., & Frame, D. (2006). Climate sensitivity constrained by temperature reconstructions over the past seven centuries. *Nature*, 440, 1029–1032. <https://doi.org/10.1038/nature04679>
- Hegerl, G. C., Hasselmann, K., Cubasch, U., Mitchell, J. F. B., Roeckner, E., Voss, R., & Waszkewitz, J. (1997). Multi-fingerprint detection and attribution analysis of greenhouse gas, greenhouse gas-plus-aerosol and solar forced climate change. *Climate Dynamics*, 13, 613–634. <https://doi.org/10.1007/s003820050186>
- Hegerl, G. C., Hoegh-Guldberg, O., Casassa, G., Hoerling, M., Kovats, S., Parmesan, C., ... Stott, P. (2010). Good practice guidance paper on detection and attribution related to anthropogenic climate change. In T. Stoker, C. Field, & Q. Dahe (Eds.), *Meeting Report of the Intergovernmental Panel on Climate Change Expert Meeting on Detection and Attribution of Anthropogenic Climate Change*. Bern, Switzerland: IPCC Working Group I Technical Support Unit, University of Bern.
- Hegerl, G. C., Karl, T. R., Allen, M., Bindoff, N. L., Gillett, N., Karoly, D., ... Zwiers, F. (2006). Climate change detection and attribution: Beyond mean temperature signals. *Journal of Climate*, 19, 5058–5077. <https://doi.org/10.1175/JCLI3900.1>
- Hegerl, G., Luterbacher, J., González-Rouco, F., Tett, S. F. B., Crowley, T., & Xoplaki, E. (2011). Influence of human and natural forcing on European seasonal temperatures. *Nature Geosciences*, 4, 99–103. <https://doi.org/10.1038/ngeo1057>
- Hegerl, G. C., & Zwiers, F. (2011). Use of models in detection and attribution of climate change. *WIREs Climate Change*, 2, 570–591. <https://doi.org/10.1002/wcc.121>
- Helland, I. P., Finstad, A. G., Forseth, T., Hesthagen, T., & Ugedal, O. (2011). Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology*, 80, 359–547. <https://doi.org/10.1111/j.1365-2656.2010.01793.x>
- Henne, P. D., Bigalke, M., Büntgen, U., Colombaroli, D., Conedera, M., Feller, U., ... Tinner, W. (2018). An empirical perspective for understanding climate change impacts in Switzerland. *Regional Environmental Change*, 18, 205–221. <https://doi.org/10.1007/s10113-017-1182-9>
- Hurrell, J. W., Holland, M. M., Gent, P. R., Ghan, S., Kay, J. E., Kushner, P. J., ... Marshall, S. (2013). The community earth system model: A framework

- for collaborative research. *Bulletin of the American Meteorological Society*, 94, 1339–1360. <https://doi.org/10.1175/BAMS-D-12-00121.1>
- Ionides, E. L., Breto, C., & King, A. A. (2006). Inference for nonlinear dynamical systems. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 18438–18443. <https://doi.org/10.1073/pnas.0603181103>
- Johnson, D. M., Bjørnstad, O. N., & Liebhold, A. M. (2004). Landscape geometry and traveling waves in the larch budmoth. *Ecology Letters*, 7, 967–974. <https://doi.org/10.1111/j.1461-0248.2004.00659.x>
- Johnson, D. M., Büntgen, U., Kausrud, K., Frank, D. C., Haynes, K. J., Liebhold, A. M., ... Stenseth, N. C. (2010). Climate change forces elevation shift in outbreak epicenter of larch budmoth. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 20576–20581.
- Johnson, E. A., & Miyanishi, K. (2008). Testing the assumptions of chronosequences in succession. *Ecology Letters*, 11, 419–431. <https://doi.org/10.1111/j.1461-0248.2008.01173.x>
- Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, 348, aaa2478. <https://doi.org/10.1126/science.aaa2478>
- Knutson, T. (2017). Detection and attribution methodologies overview. In D. J. Wuebbles, D. W. Fahey, K. A. Hibbard, D. J. Dokken, B. C. Stewart, & T. K. Maycock (Eds.), *Climate science special report: Fourth National Climate Assessment* (Vol. I, pp. 443–451). Washington, DC: U.S. Global Change Research Program.
- Knutson, T., Kossin, J. P., Mears, C., Perlwitz, J., & Wehner, M. F. (2017). Detection and attribution of climate change. In D. J. Wuebbles, D. W. Fahey, K. A. Hibbard, D. J. Dokken, B. C. Stewart, & T. K. Maycock (Eds.), *Climate science special report: Fourth National Climate Assessment* (Vol. I, pp. 114–132). Washington, DC: U.S. Global Change Research Program.
- Konter, O., Esper, J., Liebhold, A., Kyncl, T., Schneider, L., Dürthorn, E., & Büntgen, U. (2015). Tree-ring evidence for the historical absence of cyclic larch bud moth outbreaks in the Tatra Mountains. *Trees, Structure and Function*, 29, 809–814. <https://doi.org/10.1007/s00468-015-1160-0>
- Kumar, S., Zwiers, F., Dirmeyer, P. A., Lawrence, D. M., Shrestha, R., & Werner, A. T. (2016). Terrestrial contribution to the heterogeneity in hydrological changes under global warming. *Water Resource Research*, 52, 3127–3142. <https://doi.org/10.1002/2016WR018607>
- Lafferty, K. D. (2009). The ecology of climate change and infectious disease. *Ecology*, 90, 888–900.
- Lean, J. L., & Rind, D. H. (2008). How natural and anthropogenic influences alter global and regional surface temperatures: 1889 to 2006. *Geophysical Research Letters*, 35, L18701. <https://doi.org/10.1029/2008GL034864>
- Lehner, F., Schurer, A. P., Hegerl, G. C., Deser, C., & Frölicher, T. L. (2016). The importance of ENSO phase during volcanic eruptions for detection and attribution. *Geophysical Research Letters*, 43, 2851–2858. <https://doi.org/10.1002/2016GL067935>
- Lenton, T. M., Held, H., Kriegler, E., Hall, J. W., Lucht, W., Rahmstorf, S., & Schellnhuber, H. J. (2008). Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 1786–1793. <https://doi.org/10.1073/pnas.0705414105>
- Ljungqvist, F. C., Tegel, W., Krusic, P. J., Seim, A., Gschwind, F. M., Haneca, F., ... Büntgen, U. (2018). Linking European building activity with plague history. *Journal of Archaeological Science*, 98, 81–92. <https://doi.org/10.1016/j.jas.2018.08.006>
- Marini, L., Økland, B., Jönsson, A. M., Bentz, B., Carroll, A., Forster, B., ... Schroeder, M. (2017). Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography*, 40, 1426–1435. <https://doi.org/10.1111/ecog.02769>
- Masson-Delmotte, V., Schulz, M., Abe-Ouchi, A., Beer, J., Ganopolski, A., González-Rouco, J. F., ... Timmermann, A. (2013). Information from Paleoclimate Archives. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 383–464). Cambridge, UK and New York, NY: Cambridge University Press. <https://doi.org/10.1017/CBO9781107415324.013>
- Melo-Aguilar, C., González-Rouco, J. F., García-Bustamante, E., Navarro-Montesinos, J., & Steinert, N. (2018). Influence of radiative forcing factors on ground-air temperature coupling during the last millennium: Implications for borehole climatology. *Climate of the Past*, 14, 1583–1606. <https://doi.org/10.5194/cp-14-1583-2018>
- Milkoreit, M., Hodbod, J., Baggio, J., Benessaiah, K., Calderón-Contreras, R., Donges, J. F., ... Werners, S. E. (2018). Defining tipping points for social-ecological systems scholarship – An interdisciplinary literature review. *Environmental Research Letters*, 13, 033005. <https://doi.org/10.1088/1748-9326/aaa75>
- Mohan, J. E., Ziska, L. H., Schlesinger, W. H., Thomas, R. B., Sicher, R. C., George, K., & Clark, J. S. (2006). Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO₂. *Proceedings of the National Academy of Sciences of the United States of America*, 103(24), 9086–9089. <https://doi.org/10.1073/pnas.0602392103>
- Moore, J. C. (2018). Predicting tipping points in complex environmental systems. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 635–636. <https://doi.org/10.1073/pnas.1721206115>
- Moser, L., Fonti, P., Büntgen, U., Franzen, J., Esper, J., Luterbacher, J., & Frank, D. (2010). Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. *Tree Physiology*, 30, 225–233. <https://doi.org/10.1093/treephys/tpp108>
- Obermeier, W. A., Lehnert, L. W., Ivanov, M. A., Luterbacher, J., & Bendix, J. (2018). Reduced summer aboveground biomass in temperate C3 grasslands under climate change regimes. *Earth's Future*, 6, 716–729.
- Obermeier, W. A., Lehnert, L. W., Kammann, C. I., Müller, C., Luterbacher, J., Erbs, M., ... Bendix, J. (2017). Reduced CO₂ fertilization in temperate C3 grasslands towards more extreme weather conditions. *Nature Climate Change*, 7, 137–141.
- Otto, I. M., Donges, J. F., Cremades, R., Bhowmik, A., Hewitt, R. J., Lucht, W., ... Schellnhuber, H. J. (2020). Social tipping dynamics for stabilizing Earth's climate by 2050. *Proceedings of the National Academy of Sciences of the United States of America*, 117(5), 2354–2365. <https://doi.org/10.1073/pnas.1900577117>
- Otto-Bliesner, B. L., Brady, E. C., Fasullo, J., Jahn, A., Landrum, L., Stevenson, S., ... Strand, G. (2016). Climate variability and change since 850 CE: An ensemble approach with the Community Earth System Model. *Bulletin of the American Meteorological Society*, 97, 735–754. <https://doi.org/10.1175/BAMS-D-14-00233.1>
- Parmesan, C., Duarte, C., Poloczanska, E., Richardson, A. J., & Singer, M. C. (2011). Overstretching attribution. *Nature Climate Change*, 1, 2–4. <https://doi.org/10.1038/nclimate1056>
- Peters, R. L., Klesse, S., Fonti, P., & Frank, D. C. (2017). Contribution of climate vs. larch budmoth outbreaks in regulating biomass accumulation in high-elevation forests. *Forest, Ecology and Management*, 401, 147–158. <https://doi.org/10.1016/j.foreco.2017.06.032>
- Peura, M., Silveyra Gonzalez, R., Müller, J., Heurich, M., Vierling, L. A., Mönkkönen, M., & Bässler, C. (2016). Mapping a 'cryptic kingdom': Performance of lidar derived environmental variables in modelling the occurrence of forest fungi. *Remote Sensing of the Environment*, 186, 428–438. <https://doi.org/10.1016/j.rse.2016.09.003>
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., ... Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, 3, 919–925. <https://doi.org/10.1038/nclimate1958>
- Rohr, J. R., Dobson, A. P., Johnson, P. T. J., Kilpatrick, A. M., Paull, S. H., Raffel, T. R., ... Thomas, M. B. (2011). Frontiers in climate

- change-disease research. *Trends in Ecology & Evolution*, 26, 270–277. <https://doi.org/10.1016/j.tree.2011.03.002>
- Rolland, C., Baltensweiler, W., & Petitcolas, V. (2001). The potential for using *Larix decidua* ring widths in reconstructions of larch budmoth (*Zeiraphera diniana*) outbreak history: Dendrochronological estimates compared with insect surveys. *Trees, Structure and Function*, 15, 414–424. <https://doi.org/10.1007/s004680100116>
- Rosenzweig, C., & Neofotis, P. (2013). Detection and attribution of anthropogenic climate change impacts. *Wiley Interdisciplinary Reviews: Climate Change*, 4, 121–150. <https://doi.org/10.1002/wcc.209>
- Sanchez-Salguero, R., Camarero, J. J., Gutierrez, E., Gonzalez-Rouco, J. F., Gazol, A., Sanguesa-Barreda, G., ... Seftigen, K. (2017). Assessing forest vulnerability to climate warming using a process-based model of tree growth: Bad prospects for rear-edges. *Global Change Biology*, 23, 2705–2719. <https://doi.org/10.1111/gcb.13541>
- Saulnier, M., Roques, A., Guibal, F., Rozenberg, P., Saracco, G., Corona, C., & Edouard, J. L. (2017). Spatiotemporal heterogeneity of larch budmoth outbreaks in the French Alps over the last 500 years. *Canadian Journal of Forest Research*, 47, 667–680. <https://doi.org/10.1139/cjfr-2016-0211>
- Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., ... Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, 354, aaf7671-1. <https://doi.org/10.1126/science.aaf7671>
- Schmid, B. V., Büntgen, U., Easterday, W. R., Ginzler, C., Walløe, L., Bramanti, B., & Stenseth, N. C. (2015). Climate-driven introduction of the Black Death and successive plague reintroductions into Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 3020–3025. <https://doi.org/10.1073/pnas.1412887112>
- Schmidt, G. A., Jungclaus, J. H., Ammann, C. M., Bard, E., Braconnot, P., Crowley, T. J., ... Vieira, L. E. A. (2011). Climate forcing reconstructions for use in PMIP simulations of the Last Millennium (v1.1). *Geoscientific Model Development*, 4, 33–45.
- Schurer, A. P., Hegerl, G. C., Luterbacher, J., Brönnimann, S., Cowan, T., Tett, S. F. B., ... Timmreck, C. (2019). Disentangling the causes of the 1816 European year without a summer. *Environmental Research Letters*, 14, 094019. <https://doi.org/10.1088/1748-9326/ab3a10>
- Schurer, A. P., Hegerl, G. C., Mann, M. E., Tett, S. F. B., & Phipps, S. J. (2013). Separating forced from chaotic climate variability over the past millennium. *Journal of Climate*, 26, 6954–6973. <https://doi.org/10.1175/JCLI-D-12-00826.1>
- Schurer, A. P., Tett, S. F. B., & Hegerl, G. C. (2014). Small influence of solar variability on climate over the past millennium. *Nature Geoscience*, 7, 104–108. <https://doi.org/10.1038/ngeo2040>
- Shishov, V. V., Tychkov, I. I., Popkova, M. I., Ilyin, V. A., Bryukhanova, M. V., & Kiryanov, A. V. (2016). VS-oscilloscope: A new tool to parameterize tree radial growth based on climate conditions. *Dendrochronologia*, 39, 42–50. <https://doi.org/10.1016/j.dendro.2015.10.001>
- St. George, S. (2014). An overview of tree-ring width records across the Northern Hemisphere. *Quaternary Science Reviews*, 95, 132–150. <https://doi.org/10.1016/j.quascirev.2014.04.029>
- Steffen, W., Rockström, J., Richardson, K., Lenton, T. M., Folke, C., Liverman, D., ... Schellnhuber, H. J. (2018). Trajectories of the Earth system in the Anthropocene. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 8252–8259. <https://doi.org/10.1073/pnas.1810141115>
- Steinbauer, M. J., Grytnes, J. A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., ... Björkman, A. D. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556, 231–234.
- Stone, D., Auffhammer, M., Carey, M., Hansen, G., Huggel, C., Cramer, W., ... Yohe, G. (2013). The challenge to detect and attribute effects of climate change on human and natural systems. *Climatic Change*, 121, 381–395. <https://doi.org/10.1007/s10584-013-0873-6>
- Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CIMP5 and the experiment design. *Bulletin of the American Meteorological Society*, 93, 485–498.
- Tegel, W., Hakelberg, D., Elbrüg, R., Stäuble, H., & Büntgen, U. (2012). Early Neolithic water wells reveal the world's oldest wood architecture. *PLoS ONE*, 7, e51374. <https://doi.org/10.1371/journal.pone.0051374>
- Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., & Araujo, M. B. (2011). Consequences of climate change on the tree of life in Europe. *Nature*, 470, 531–534. <https://doi.org/10.1038/nature09705>
- Turchin, P., Wood, S. N., Ellner, S. P., Kendall, B. E., Murdoch, W. W., Fischlin, A., ... Briggs, C. J. (2003). Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. *Ecology*, 84, 1207–1214. [https://doi.org/10.1890/0012-9658\(2003\)084\[1207:DEOPQA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1207:DEOPQA]2.0.CO;2)
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11, 1351–1363. <https://doi.org/10.1111/j.1461-0248.2008.01250.x>
- Vierling, K. T., Vierling, L. A., Gould, W. A., Martinuzzi, S., & Clawges, R. M. (2008). Shedding new light on habitat characterization and modelling. *Frontiers in Ecology and the Environment*, 6, 90–98.
- Wang, J., Yang, B., Ljungqvist, F. C., Luterbacher, J., Osborn, T. J., Briffa, K. R., & Zorita, E. (2017). Internal and external forcing of multidecadal Atlantic climate variability over the past 1,200 year. *Nature Geoscience*, 10, 512–517.
- Wang, J., Yang, B., Osborn, T. J., Ljungqvist, F. C., Zhang, H., & Luterbacher, J. (2018). Causes of East Asian temperature multidecadal variability since 850 CE. *Geophysical Research Letters*, 45, 13485–13494. <https://doi.org/10.1029/2018GL080725>
- Wassmann, P., & Lenton, T. M. (2012). Arctic tipping points in an Earth system perspective. *Ambio*, 41, 1–9. <https://doi.org/10.1007/s13280-011-0230-9>
- Williamson, M. S., Bathiany, S., & Lenton, T. M. (2016). Early warning signals of tipping points in periodically forced systems. *Earth Systems Dynamics*, 7, 313–326. <https://doi.org/10.5194/esd-7-313-2016>
- Wolf, A., Field, C. B., & Berry, J. A. (2011). Allometric growth and allocation in forests: A perspective from FLUXNET. *Ecological Applications*, 21, 1546–1556. <https://doi.org/10.1890/10-1201.1>
- Yuan, N., Moser, G., Müller, C., Obermeier, W. A., Bendix, J., & Luterbacher, J. (2018). Extreme climatic events down-regulate the grassland biomass response to elevated carbon dioxide. *Nature Science Reports*, 8, 17758. <https://doi.org/10.1038/s41598-018-36157-x>
- Zhang, X., Zwiers, F. W., Hegerl, G. C., Gillett, N., Lambert, H., Solomon, S., ... Nozawa, T. (2007). Detection of human influence on twentieth-century precipitation trends. *Nature*, 448, 461–465. <https://doi.org/10.1038/nature06025>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Büntgen U, González-Rouco JF, Luterbacher J, Stenseth NC, Johnson DM. Extending the climatological concept of 'Detection and Attribution' to global change ecology in the Anthropocene. *Funct Ecol*. 2020;00:1–13. <https://doi.org/10.1111/1365-2435.13647>