Climatic extremes improve predictions of spatial patterns of tree species

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Understanding niche evolution, dynamics, and the response of species to climate change requires knowledge of the determinants of the environmental niche and species range limits. Mean values of climatic variables are often used in such analyses. In contrast, the increasing frequency of climate extremes suggests the importance of understanding their additional influence on range limits. Here, we assess how measures representing climate extremes (i.e., interannual variability in climate parameters) explain and predict spatial patterns of 11 tree species in Switzerland. We find clear, although comparably small, improvement (+20% in adjusted D^2, +8% and +3% in cross-validated True Skill Statistic and area under the receiver operating characteristics curve values) in models that use measures of extremes in addition to means. The primary effect of including information on climate extremes is a correction of local overprediction and underprediction. Our results demonstrate that measures of climate extremes are important for understanding the climatic limits of tree species and assessing species niche characteristics. The inclusion of climate variability likely will improve models of species range limits under future conditions, where changes in mean climate and increased variability are expected.

climate change | ecological niche | generalized additive model | geographic range | species distribution models

The understanding of the principles and mechanisms that shape distribution patterns has long been a focus in biogeographical, ecological, and evolutionary research. The ecological niche concept, coined and initially developed by Grinnell (1), is the foundation for our understanding of the processes that shape the geographical distributions of species (2). Conceptual clarifications with regards to using the concept for the explanation of species ranges have been presented by several authors (3, 4). Climatic variables are often used to predict biogeographical patterns (5), and considerable effort has been put into improving methods to describe the response of species along climate gradients (6–8). These methods of species distribution or niche modeling are frequently used for conservation management (9–12), prediction of the likely effects of global change (13–16), and, increasingly, assessment of niche characteristics in the study of niche evolution (17–20). These studies in general use monthly or annual climatic means to analyze species distribution patterns. To date, little attention has been paid to the question of how climatic extremes, i.e., the long-term, interannual variation around mean values, could help to explain species distributions. There are two major reasons that highlight the importance of including climatic variability in niche analyses and models. First, ongoing climate change not only affects means but also extremes (21). Second, niche evolution often results in changes of the stress tolerance of evolving clades (22, 23). Thus, both adaptation and possible future response of species to climate are certainly affected by extremes in addition to means.

On a more fundamental level, the question is what aspects of climate actually determine the "climate response" of plant species. The expected effects of climate extremes are diverse. At the range limit of species, source-sink dynamics likely exert strong influence (3, 24–26). In sessile organisms like plants, extremely adverse climate can constrain regeneration and impact range limits through increased mortality (27). Extremely favorable climate, in contrast, might allow unusually high reproductive success or the advance of range limits, especially when such effects occur over several years. The observed effects of severe heat and drought illustrate such range contractions at the trailing edge of species ranges. Such effects are visible by the dieback of Scots pine (*Pinus sylvestris* L.) in the warmest part of the dry valleys of the European Alps and increased diebacks in conifers in western North America (28) that are likely caused by recent warming and increased drought. Ongoing climate change impacts species phenology (29), individual growth (30), and ecosystem dynamics (31, 32). In addition, species have experienced recent range shifts (33–35), some of which are clearly induced by climatic extremes (36), whereas other responses seem more gradual (37). In particular, climatic extremes can be responsible for dieback at the trailing edge of species distributions (38). These examples illustrate the potential importance of including climatic variability into analyses and models.

Climate variability alone likely does not explain the climatic response of species very well. Rather, variability may complement a species' response to mean climate, which summarizes complex mechanisms that are not directly expressed in a fitted response curve. For instance, under optimal temperature or moisture conditions, climatic variability or extremes could have relatively little effect on species, whereas the effect of variability is likely severe where mean temperature or water availability is closer to physiological tolerances. In contrast, under conditions in which warm temperatures and abundant moisture are favorable for growth, the effects of competition (on abundance, reproductive success, etc.) may outweigh the direct effects of climate. For example, a species' range might in some areas be directly limited by physiological tolerance to low temperatures, whereas in other areas with relatively warm climate, the range

Fig. 1. Conceptual graph explaining possible effects of climatic and biotic constraints of species niches (**A**) with its effects on range limits along simple gradients of climatic means. The response shape typically fitted by regression-type models along gradients of mean climates is given as unimodal curves. Additionally, we illustrate the likely more local (with respect to ecological and spatial gradients) effect of extremes and biotic interactions as causal drivers of a reduction in the mean response along the same mean gradient. Zone **a** of the observed distribution in environmental space thus may represent areas where a species occurs close to the fundamental niche, whereas zone **i** does not give an indication of fundamental niche constraints, and the distribution may then be rather constrained by biotic interactions.

limit is caused not by an excess of heat, but by competition (refs. 39 and 40 and Fig. 1). Thus, gradients of mean climate likely integrate both physiological constraints (effected at certain climatic extremes) and the gradual competitive replacement of one species by another (41).

Here, we examine whether climatic extremes help to explain patterns of tree species distributions compared with using climatic means alone. We tested whether this effect is stronger when interactions between means and extremes are modeled. We report tests using data from 12,328 forest plots in Switzerland, where climatic extremes and long-term means were calculated for each plot for a 47-year period by using daily climate estimates. We developed generalized additive models (GAMs) for each of 11 abundant tree species to test our hypotheses. The effects of extreme climatic events were analyzed by using specific approaches based on extreme value statistics (42). Frequencies of extreme events are, however, sensitive to the mean and even more to the variability of climatic variables at a given location (43, 44). Thus, adding as predictor variables indices of extreme events to models that include mean values would confound the effects of mean and variability. Therefore, we used the standard deviation of monthly climate variables to express information on extremes additional to that on means. Collinearity problems were therefore much reduced, because measures of variability are less correlated with means than are extremes expressed as quantiles or absolute extremes. Our long-term temporal variability measures are also fundamentally different from variability parameters available in the Worldclim dataset (45), because these measures capture intraannual variability calculated from long-term monthly means. We focus on interyear variability in extremes. If our hypotheses are supported, inclusion of climatic extremes might help to forecast effects of climate change and assess adaptive niche evolution.

Results

We found a significant improvement (ANOVA, χ^2 test; see Table S1 in *SI Appendix*) in the calibration of the nonparametric

Fig. 2. Comparison of 10-fold cross-validated model performance (TSS, AUC) when using climate means (light blue) vs. means and extremes (purple) climate predictors in GAMs predicting the spatial patterns of 11 tree species. Species names are abbreviated, and the full names are given in Table S1 in *SI Appendix*. With the exception of *P. abies*, all species more or less clearly increase their predictive capacity.

GAMs of species distributions when using climatic variability as predictors compared with using average climate variables alone (Fig. 2). The fit of models for the 11 species, as measured by the True Skill Statistic (TSS) (46) from 10-fold cross-validation, was better when we included variables representing both climate means and extremes [0.548 ± 0.036 (mean ± SE)] than when only climate means were represented (−0.040 ± 0.0038), a significant difference (two-tailed Wilcoxon signed rank test, $V = 0$, $P = 0.001$). This improvement was also true when we evaluated model fit with area under the receiver operating characteristics curve (AUC) (variables representing mean and extremes: 0.843 ± 0.016; mean only: −0.025 ± 0.017; $V = 1$, $P = 0.002$; Fig. 3 and Table S2 in *SI Appendix*). The results were similar when we included the interaction of variables representing climatic means and extremes instead of only adding climatic extremes variables. We observed again a significant improvement of each model in an ANOVA test compared with using climatic means alone

Fig. 3. Comparison of the influences of two tested predictor types in nonparametric GAMs using 10-fold cross-validated model performance (TSS, AUC) for 11 tree species. When adding measures of extremes to mean climatic predictors (maroon), the average model performance and the accuracy of the least performing models increase compared with using only climatic means (steel blue).

Fig. 4. Predicted probabilities for *F. sylvatica* along major climate gradients. (*A* and *B*) Illustration of fitted probabilities for *F. sylvatica* when using only mean climate predictors (*A*) compared with using means and standard deviations without statistical interaction term (*B*). (*C* and *D*) The probabilities from the model using means and standard deviations are plotted against TAWI.avg and TAWI.std (*C*) and against MISU.avg and MISU.std (*D*). Light gray and black dots represent all plots and plots where *F. sylvatica* is present, respectively. Blue and magenta represent low and high model probabilities, respectively, as indicated by the contour lines.

(Fig. S1 in *SI Appendix*). The overall improvement in cross-validated model performance was significant (TSS: interactions of variables representing means and extremes: 0.561 ± 0.034; mean only: -0.052 ± 0.038; $V = 0$, $P = 0.001$; AUC: interactions of mean and extreme variables: 0.848 ± 0.015; mean only: -0.030 ± 0.015; $V = 0$, $P = 0.001$). Adjusted D^2 increased by 20%, whereas TSS and AUC increased by 8% and 3%, respectively. However, when comparing the two versions of implementing extremes into models, we found that in 4 (*Acer pseudoplatanus*, *Pinus sylvestris*, *Quercus robur*, and *Betula pendula*) of the 11 species no significant improvement was reached in the ANOVA tests (Fig. S1 in *SI Appendix*). Only the overall improvement in cross-validated model accuracies was significant (TSS: interactions of mean and extreme variables: 0.561 ± 0.034; no interaction of mean and extreme variables: -0.012 ± 0.036; $V = 8$, $P = 0.024$; AUC: interactions of mean and extreme variables: 0.848 ± 0.015; no interaction of mean and extreme variables: -0.006 ± 0.016; $V = 9$, $P = 0.032$).
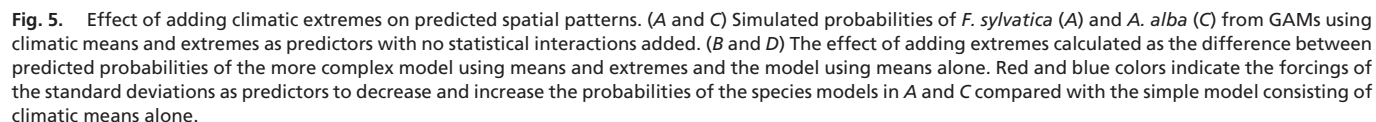
When adding variables representing extremes to models using climatic means for predicting spatial patterns of tree species, we note a shift in the probability space of *Fagus sylvatica* (Fig. 4). The species becomes less limited toward warmer temperatures and the limitation toward cold temperatures depends less on water availability (Fig. 4*B*). In the geographic space, adding variables representing extremes translates into a correction of predictions from the model using means only, especially in the dry and Mediterranean (Southern) parts of Switzerland (Fig. 5 *A* and *B*) for *F. sylvatica*. Including climate variability in the models of *Abies alba* (Fig. 5 *C* and *D*) increases prediction probabilities in the comparably moist climates of central and western Switzerland and further reduces the spatial distribution in the southern part of the Alps and in the central valleys with comparably dry climates. Presence/absence information for all tree species is given in Fig. S2 in *SI Appendix*; results for all 11 species are given in Fig. S3 in *SI Appendix*.

Discussion

Our analyses reveal that complementing mean climate predictors with variables that represent climate extremes yields an improvement in the predictive power of species distribution models. The improvement is small compared with the model using climatic means only and specifically corrects spatial predictions compared with using climate means alone. This small improvement is partly in agreement with early investigations regarding explanations of distribution range patterns in trees and other plants. Larcher and Mair (47) observed that absolute climatic extremes alone are incapable of explaining the northern range limits of (climate constrained) Mediterranean oak species. They argued that average (winter) temperatures are more suitable for explaining northern range limits. We found, however, that adding climatic variability helps to explain such range limits. Another example involves the quest for a climatic explanation of the upper treeline worldwide. Current explanations focus on average climate predictors (48), and the best model based on a global dataset of mountain treeline temperatures reveals a strong relationship between treeline and average summer temperatures (49, 50). However, no explanation that we examined included additional effects of climate variability.
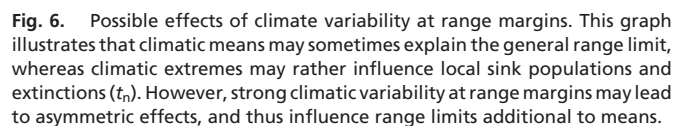
The effect of extremes and means are not easy to separate because of the high correlation between mean values and percentiles as measures of extremes. We expect that higher frequency or severity of extremes affect range margins in plants. Clear evidence exists that severe climate extremes influence plant demographic processes, such as growth (30, 32), regeneration (51), and mortality (38, 52, 53). However, it is not immediately evident from these studies that the observed responses affect range limits directly. Such processes may simply result in strong source-sink dynamics at range edges, with the range limit resulting from complex and multiple interactions (24, 54). For example, there may be strong mortality patterns after dry or cold years in tree saplings, but even a complete failure of

Fig. 5. Effect of adding climatic extremes on predicted spatial patterns. (*A* and *C*) Simulated probabilities of *F. sylvatica* (*A*) and *A. alba* (*C*) from GAMs using climatic means and extremes as predictors with no statistical interactions added. (*B* and *D*) The effect of adding extremes calculated as the difference between predicted probabilities of the more complex model using means and extremes and the model using means alone. Red and blue colors indicate the forcings of the standard deviations as predictors to decrease and increase the probabilities of the species models in *A* and *C* compared with the simple model consisting of climatic means alone.

recruitment in particularly adverse years may not impact the species range limit, but instead primarily affect age structure and source-sink dynamics (55, 56). The demographic signal of extreme adverse and favorable events may lead to both positive (range expansion, regeneration) and negative (range contraction, mortality) effects locally. The resulting patterns of overall range limits may well reflect climatic means (Fig. 6). However, when the variability around means is very high, then a species may not be able to compensate in good years the losses that occur during adverse years. Climate variability, in addition to means, then clearly affects range limits.

The association of range margin and climatic mean may not hold when climatic extremes occur with a skewed frequency distribution where the mean slowly shifts in a single direction, as during current, ongoing climatic change (57). In this situation mortality and regeneration are increasingly affected by climatic

extremes rather than by means (28, 38, 58). Thus, projections of species responses to climate change might benefit from calibrating models to both climate means and extremes (expressed as variability). This addition could be especially important for forecasting the trailing edge of shifting ranges (59). Evaluation of the differences in forecasts that are based on climate means and variables representing extremes could contribute to better assessment of forecasting uncertainty. In our example with *F. sylvatica* and *A. alba*, a reduction in predicted probability at the warm end of the current distribution occurred when adding variables representing climatic extremes to the model calibration. The challenge remains to cover sufficient climatic variability during sampling to span the range of climatic variation that is expected in the future. Ongoing climate change, however, could also reduce the sensitivity of species distribution patterns to climatic extremes. Such reduced sensitivities, specifically with regards to tree growth, have been observed repeatedly in the recent past (60, 61), and climate change is a likely explanation (62).

The effects of climatic extremes on limiting species distributions are likely important when climate means shift geographically and when variability changes. The daily climate surfaces we used may have smoothed climatic extremes, causing us to overlook patterns of truly extreme events. The same could also occur because of the limited temporal span of the climate data. First, such limitations are difficult to overcome, because we used a contemporary method to generate daily climate surfaces. Second, we performed initial tests to use absolute extremes instead of means, which did not improve the model fits. Third, the size of the available time window to analyze extremes over a large area is potentially problematic. Trees are long-lived and their stress tolerance differs among life stages. More information on stress tolerance at different life stages would enhance our ability to optimize analyses to the relevant time window. Other effects that reduce the sensitivity of species distributions to climate fluctuations include human influence through forest management and the possibility that observed distributions may

Fig. 6. Possible effects of climate variability at range margins. This graph illustrates that climatic means may sometimes explain the general range limit, whereas climatic extremes may rather influence local sink populations and extinctions (t_n). However, strong climatic variability at range margins may lead to asymmetric effects, and thus influence range limits additional to means.

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not be in equilibrium with current climate (63). In our dataset, we assume a strong effect of forest management on the Swiss Plateau for *Picea abies*. For most forests of dry interior valleys we expect little to no effect from management on the elevational ranges of the species we considered. Finally, we believe that some of the limitations identified in our analysis of large-scale observational data can only be overcome by experiments. Ideally, such complementary analyses combine the power of large observational datasets with the insights of careful experimental design.

Materials and Methods

Tree Distribution Data. We used data from two forest inventory periods in Switzerland, which were sampled during the years 1983–1985 (NFI1) and 1995–1997 (NFI2) on a regular 1-km grid. In total, we had 12,328 plots available where species presence and absence for >50 species was derived from basal area estimates. The inventory records a total of >50 tree species, of which we selected 11 species for modeling. The selected species are (*i*) sufficiently abundant, (*ii*) belong to two different functional groups [broadleaf deciduous: *Fagus sylvatica* L., *Acer pseudoplatanus* L., *Fraxinus excelsior* L., *Quercus petraea* (Mattuschka) Lieblein, *Q. robur* L., *Sorbus aria* (L.) Crantz, *Betula pendula* Roth; needleleaf evergreen: *Picea abies* (L.) H. Karsten, *Abies alba* Miller, *Pinus sylvestris* L., *P. cembra* L.], and (*iii*) cover the full elevational gradient available in Switzerland from 180 m above seal level (a.s.l.) to the treeline situated at ≈2,450 m a.s.l. in the dry interior valleys. Additional details regarding the forest inventory data are given in *SI Appendix*.

Climate Predictor Data. We generated a climate predictor set containing long-term (1961–2006) averages of monthly, seasonal, or annual predictors and standard deviations of the mean values representing extremes. These estimates were derived at a spatial resolution of 100 m by using the DAYMET algorithm (64). We used data from automated weather stations (>180 for temperature; >350 for precipitation provided by MeteoSwiss) and a 100-m digital elevation model from the Swiss National Office of Topography. DAYMET generates output for daily average, minimum, and maximum temperature and precipitation. Additionally, we calculated potential evapotranspiration, and moisture index, which is the difference between precipitation and potential evapotranspiration (65). For the methods for deriving these two variables, see ref. 66. Additional to these climate predictors, we added slope and topographic position to the lists of evaluated predictors. More information on the derivation of the climate predictors is given in *SI Appendix*, and high and low mean and standard deviations of the selected climate variables are presented in Fig. S1 in *SI Appendix*.

Extreme climatic events are best analyzed by using specific approaches based on extreme value statistics (42). Frequencies of extreme events are, however, sensitive to the mean and even more to the variability of climatic variables at a given location (43, 44). Thus, adding extreme event indices as predictor variables to a model including the mean values would confound the effects of mean and variability. Therefore, we chose standard deviations as expressions of extremes in combination with means. We did this for three additional reasons, namely: (*i*) single-day or rare extremes are very difficult to assess or detect, and even more so to spatially extrapolate. Standard deviations that include the likelihood of extreme events are much easier to extrapolate and to measure. (*ii*) We do not know exactly what period is relevant

regarding extremes for each individual species. They are different in size and age, and the relevant period of sensitivity may change. Thus, a measure of variability (in combination with means) is more likely to capture the general likelihood of extreme events relevant to individual species than do single few observations. Variability can be calculated quite accurately from the whole time series. (*iii*) There is a high correlation between mean and extremes (percentiles). Thus, adding both means and percentiles as expressions of extremes would result in severe collinearity problems when fitting models.

For our model exercise with the selected tree species we chose two climatic variables, namely: (*i*) average winter temperature (TAWI: December, January, February), and (*ii*) average summer moisture index (MISU: June, July, August). TAWI (°C) expresses winter cold limitations, whereas MISU (mm) expresses water availability and levels of drought stress. For these two variables, we calculated both means and standard deviations. Additionally, we added slope and topographic position (66). The six selected variables show very low correlations on average (0.254), and only two variables correlate >0.5 (mean and SD of MISU: 0.73).

Statistical Analyses. We chose GAMs as implemented in the R package *mgcv* (67). This is a flexible, nonparametric method for calibrating the species response to topo-climatic predictors, which allowed us to additionally test the effect of interactions between means and standard deviations by using smooth terms built with tensor products (68). In *mgcv*, the degrees of smoothing are selected by internal cross-validations. All variables were entered in the default mode, and three models were finally calibrated for each species. The first used all selected variables except the two standard deviations, whereas the second included the two standard deviations. The third used interaction terms from tensor product smoothed terms of the respective mean and standard deviations (MISU and TAWI), instead of adding the two variables separately.

All models were 10-fold cross-validated and model performance of calibrated and cross-validated models was analyzed by calculating the adjusted D^2 (see ref. 5), threshold-maximized TSS (46) and AUC (69), which allows assessment of model accuracy independent of thresholds. The model improvement when adding extremes in addition to means was tested in two ways. First, we performed an ANOVA using a χ^2 test for checking the significance of the improvement in calibration strength. Second, we tested the improvement in model quality by applying a paired Wilcoxon test to the model evaluation values (TSS, AUC) of all species' models with means only against all species' models with means and extremes. The first (ANOVA) test allowed us to evaluate the individual improvement of models, whereas the second (Wilcoxon) test allowed us to evaluate the overall improvement of the predictive power of the models. All analyses were performed in the statistical environment R (70).

1. Grinnell J (1917) The niche relationships of the California Thrasher. *Auk* 34:427–433.
2. Chase JM, Leibold MA (2003) *Ecological Niches: Linking Classical and Contemporary Approaches* (Chicago Univ Press, Chicago), 1st Ed.
3. Pulliam HR (2000) On the relationship between niche and distribution. *Ecol Lett* 3:349–361.
4. Soberón J, Nakamura M (2009) Niches and distributional areas: Concepts, methods, and assumptions. *Proc Natl Acad Sci USA* 106:19644–19650.
5. Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186.
6. Austin MP (1987) Models for the analysis of species' response to environmental gradients. *Vegetation* 69:35–45.
7. Elith J, et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
8. Thuiller W (2003) BIOMOD: Optimizing predictions of species distributions and projecting potential future shifts under global change. *Glob Change Biol* 9:1353–1362.
9. Hannah L, et al. (2007) Protected area needs in a changing climate. *Front Ecol Environ* 5:131–138.
10. Peralvo M, Sierra R, Young KR, Ulloa-Ulloa C (2007) Identification of biodiversity conservation priorities using predictive modeling: An application for the equatorial pacific region of South America. *Biodivers Conserv* 16:2649–2675.
11. Ramirez-Bastida P, Navarro-Siguenza AG, Peterson AT (2008) Aquatic bird distributions in Mexico: Designing conservation approaches quantitatively. *Biodivers Conserv* 17:2525–2558.
12. Seo C, Thorne JH, Hannah L, Thuiller W (2009) Scale effects in species distribution models: Implications for conservation planning under climate change. *Biol Lett* 5:39–43.
13. Thomas CD, et al. (2004) Extinction risk from climate change. *Nature* 427:145–147.
14. Thuiller W, Lavorel S, Araujo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci USA* 102:8245–8250.
15. Iverson LR, Prasad AM, Matthews SN, Peters M (2008) Estimating potential habitat for 134 eastern U.S. tree species under six climate scenarios. *For Ecol Manage* 254:390–406.
16. Lawler JJ, et al. (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90:588–597.
17. Ackerly DD, Schwilk DW, Webb CO (2006) Niche evolution and adaptive radiation: Testing the order of trait divergence. *Ecology* 87:S50–S61.
18. Evans MEK, Smith SA, Flynn RS, Donoghue MJ (2009) Climate, niche evolution, and diversification of the ''bird-cage'' evening primroses (Oenothera, sections Anogra and Kleinia). *Am Nat* 173:225–240.
19. Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C (2004) Integrating phylogenetic and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution (Lawrence, Kans)* 58:1781–1793.

20. Knouft JH, Losos JB, Glor RE, Kolbe JJ (2006) Phylogenetic analysis of the evolution of the niche in lizards of the anolis sagrei group. *Ecology* 87:29–38.

21. Frei C, Schöll R, Fukutome S, Schmidli J, Vidale PL (2006) Future change of precipitation extremes in Europe: Intercomparison of scenarios from regional climate models. *J Geophys Res* 111:D06105.

22. Gavrilets S, Losos JB (2009) Adaptive radiation: Contrasting theory with data. *Science* 323:732–737.

23. Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. *Bull Am Meteorol Soc* 81:443–450.

24. Holt RD (2003) On the evolutionary ecology of species' ranges. *Evol Ecol Res* 5:159–178.

25. Holt RD (2009) Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proc Natl Acad Sci USA* 106:19659–19665.

26. Pulliam HR (1988) Sources, sinks, and population regulation. *Am Nat* 132:652–661.

27. Honnay O, et al. (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecol Lett* 5:525–530.

28. van Mantgem PJ, et al. (2009) Widespread increase of tree mortality rates in the Western United States. *Science* 323:521–524.

29. Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature* 397:659.

30. Jolly WM, Dobbertin M, Zimmermann NE, Reichstein M (2005) Divergent vegetation growth responses to the 2003 heat wave in the Swiss Alps. *Geophys Res Lett* 32:L18409.

31. Nemani RR, et al. (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300:1560–1563.

32. Ciais P, et al. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529–533.

33. Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.

34. Root TL, MacMynowski DP, Mastrandrea MD, Schneider SH (2005) Human-modified temperatures induce species changes: Joint attribution. *Proc Natl Acad Sci USA* 102:7465–7469.

35. Walther GR, et al. (2002) Ecological responses to recent climate change. *Nature* 416:389–395.

36. Walther G-R, et al. (2009) Alien species in a warmer world: Risks and opportunities. *Trends Ecol Evol*, in press.

37. Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771.

38. Bigler C, Braeker OU, Bugmann H, Dobbertin M, Rigling A (2006) Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems* 9:330–343.

39. Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: Size, shape, boundaries, and internal structure. *Annu Rev Ecol System* 27:597–623.

40. McArthur RH (1972) *Geographical Ecology: Patterns in the Distribution of Species* (Harper & Row, New York).

41. Whittaker RH, Niering WA (1965) Vegetation of the Santa Catalina Mountains, Arizona: A gradient analysis of the South Slope. *Ecology* 46:429–452.

42. Katz RW, Brush GS, Parlange MB (2005) Statistics of extremes: Modeling ecological disturbances. *Ecology* 86:1124–1134.

43. Katz RW, Brown BG (1992) Extreme events in a changing climate: Variability is more important than averages. *Clim Change* 21:289–302.

44. Mearns LO, Katz RW, Schneider SH (1984) Extreme high-temperature events: Changes in their probabilities with changes in mean temperature. *J Appl Meteorol Climatol* 23:1601–1613.

45. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high-resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978.

46. Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: Prevalence, kappa, and the true skill statistic (TSS). *J Appl Ecol* 43:1223–1232.

47. Larcher W, Mair B (1969) The temperature resistance as ecophysiological trait: 1. *Quercus ilex* and other Mediterranean oak species (Translated from German) *Oecol Plant* 4:347–376.

48. Körner C (1998) A reassessment of high-elevation treeline positions and their explanation. *Oecologia* 115:445–459.

49. Gehrig-Fasel J, Guisan A, Zimmermann NE (2008) Evaluating thermal treeline indicators based on air and soil temperature using an air-to-soil temperature transfer model. *Ecol Model* 213:345–355.

50. Körner C, Paulsen J (2004) A worldwide study of high altitude treeline temperatures. *J Biogeogr* 31:713–732.

51. Ibanez I, Clark JS, LaDeau S, HilleRisLambers J (2007) Exploiting temporal variability to understand tree recruitment response to climate change. *Ecol Monogr* 77:163–177.

52. van Mantgem PJ, Stephenson NL (2007) Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecol Lett* 10:909–916.

53. Villalba R, Veblen TT (1998) Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. *Ecology* 79:2624–2640.

54. Holt RD, Keitt TH, Lewis MA, Maurer BA, Taper ML (2005) Theoretical models of species' borders: Single species approaches. *Oikos* 108:18–27.

55. Payette S (2007) Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. *Ecology* 88:770–780.

56. Devi N, et al. (2008) Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century. *Glob Change Biol* 14:1581–1591.

57. Heino R, et al. (1999) Progress in the study of climatic extremes in northern and central Europe. *Clim Change* 42:151–181.

58. Kurz WA, et al. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452:987–990.

59. Thuiller W, et al. (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspect Plant Ecol Evol Syst* 9:137–152.

60. Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaskan white spruce in the 20th century from temperature-induced drought stress. *Nature* 405:668–673.

61. Briffa KR, et al. (1998) Reduced sensitivity of recent tree growth to temperature at high northern latitudes. *Nature* 391:678–682.

62. D'Arrigo R, Wilson R, Liepert B, Cherubini P (2008) On the divergence problem in Northern forests: A review of the tree-ring evidence and possible causes. *Glob Planet Change* 60:289–305.

63. Svenning JC, Normand S, Skov F (2008) Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography* 31:316–326.

64. Thornton PE, Running SW, White MA (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. *J Hydrol* 190:214–251.

65. Zimmermann NE, Kienast F (1999) Predictive mapping of alpine grasslands in Switzerland: Species versus community approach. *J Vegetat Sci* 10:469–482.

66. Zimmermann NE, Edwards TC, Moisen GG, Frescino TS, Blackard JA (2007) Remote sensing-based predictors improve distribution models of rare, early successional, and broadleaf tree species in Utah. *J Appl Ecol* 44:1057–1067.

67. Wood SN (2008) Fast stable direct fitting and smoothness selection for generalized additive models. *J R Stat Soc B* 70:495–518.

68. Wood SN (2006) Low rank scale invariant tensor product smooths for generalized additive mixed models. *Biometrics* 62:1025–1036.

69. Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv* 24:38–49.

70. R Development Core Team (2009) *R: A Language and Environment for Statistical Computing, Reference Index Version 2.9.2.* (R Foundation for Statistical Computing, Vienna).