# Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change

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*Abstract.* Obtaining reliable predictions of species range shifts under climate change is a crucial challenge for ecologists and stakeholders. At the continental scale, niche-based models have been widely used in the last 10 years to predict the potential impacts of climate change on species distributions all over the world, although these models do not include any mechanistic relationships. In contrast, species-specific, process-based predictions remain scarce at the continental scale. This is regrettable because to secure relevant and accurate predictions it is always desirable to compare predictions derived from different kinds of models applied independently to the same set of species and using the same raw data. Here we compare predictions of range shifts under climate change scenarios for 2100 derived from niche-based models with those of a process-based model for 15 North American boreal and temperate tree species. A general pattern emerged from our comparisons: niche-based models tend to predict a stronger level of extinction and a greater proportion of colonization than the process-based model. This result likely arises because niche-based models do not take phenotypic plasticity and local adaptation into account. Nevertheless, as the two kinds of models rely on different assumptions, their complementarity is revealed by common findings. Both modeling approaches highlight a major potential limitation on species tracking their climatic niche because of migration constraints and identify similar zones where species extirpation is likely. Such convergent predictions from models built on very different principles provide a useful way to offset uncertainties at the continental scale. This study shows that the use in concert of both approaches with their own caveats and advantages is crucial to obtain more robust results and that comparisons among models are needed in the near future to gain accuracy regarding predictions of range shifts under climate change.

*Key words: biodiversity; biogeography; climate change; extinction; migration; niche-based modeling; process-based modeling; species distribution.*

## Introduction

Numerous impacts of climate change on plants have been documented during the last 10 years (Parmesan 2006), including impacts on plant function, in particular growth (Myneni et al. 1997, Saxe et al. 2001, Korner et al. 2005) and phenology (Menzel and Fabian 1999, Root et al. 2003, Menzel et al. 2006, Schwartz et al. 2006), but also on biotic interactions (Hughes 2000, Suttle et al. 2007) and on species distributions through local extinction of populations (Parmesan 2006) and range shifts (Kullman 2002, Walther et al. 2002, 2005, Parmesan and Yohe 2003). Such impacts can cause major changes in ecosystem functioning and in biodiversity (Lovejoy and Hannah 2005). Assessing species range shifts is especially crucial for trees as they are a

major component of landscape structure, provide important services such as wood production and recreational opportunities, play a major role in forest ecosystem functioning, and provide critical habitats for many animal and plant species (Begon et al. 2005).

Evidence of accelerating climate change (IPCC 2007) heightens the urgency of obtaining accurate predictions of species range shifts in coming decades so that effective mitigation strategies can be developed to sustain ecosystem services and function (MEA 2005, Sutherland 2006). Predicting climate-driven changes in phenology and plant distribution is a key requirement to forecast future climate change because of the feedback of vegetation to the atmosphere through water, carbon, and heat fluxes (Betts et al. 1997, Sitch et al. 2003). The situation is complicated, however, because each tree species cannot be expected to experience the same impacts given differing exposure to climate change, physiological tolerance, and niche characteristics. Midgley et al. (2007) predicted that deciduous broad-leaved trees in the temperate zone will be among the most

sensitive to climate change and most in need of further study, especially because global warming is predicted to be stronger in high latitudes (IPCC 2007).

What then are the best strategies for obtaining accurate predictions for changes in the distributions of deciduous temperate trees? At the scale of the geographic distribution of species, no experiments in situ can be reasonably carried out to predict possible range shifts (Woodward 1987). Modeling therefore appears the most feasible and efficient way to establish useful predictions (Lovejoy and Hannah 2005, Thuiller 2007), and several kinds of models have been developed during the previous decade for this purpose. As reviewed by Midgley et al. (2007), these models fall into two main classes: vegetation-type models (dynamic global vegetation models [DGVMs]) and species-specific models (niche-based and process-based).

Dynamic global vegetation models (Neilson 1995, Sitch et al. 2003) use submodels for photosynthesis, plant carbon balance, and other factors to simulate the form of vegetation at a particular location but at a coarse spatial resolution when used with a spatial grid. For the sake of generality, DGVMs traditionally simulate groups of species having similar form and function in ecosystems (plant functional types; PFTs). For these reasons, they do not aim to focus on specific species distributions (or on very dominant species), although some new developments have seen the emergence of hybrid DGVM–individual-based models (e.g., LPJ-GUESS, Smith et al. 2001; HYBRID, Friend et al. 1997) focusing on particular well-known dominant species (Koca et al. 2006). However, as useful as they can be, most DGVMs focus on prediction of changes in vegetation type and are uninformative with regard to range shifts or risks of extinction for specific species (Neilson et al. 2005). Therefore we chose to dismiss this class of model for this study because they as yet cannot reach the level of precision required and they have not been calibrated yet for the species selected in this study.

Within the class of species-specific models, niche-based (NB) models in contrast rely on the establishment of statistical or theoretical relationships between environmental predictors (especially climatic ones, i.e., bioclimatic models) and observed species distributions. Species data can be simple presence, presence/absence, or abundance observations based on random or stratified field sampling or observations obtained from natural history museums. The modeled niche is then projected into the future using data from general or regional circulation models (GCM, RCM), highlighting the areas currently suitable but predicted to become unsuitable under climate change (and vice versa; Ohlemüller et al. 2006). Niche-based models have been widely used in the last 10 years to predict the potential impacts of both climate (Sykes 1996, Bakkenes et al. 2002, Sutherst 2003, Thuiller et al. 2005, 2006) and land use change (Bomhard et al. 2005) on species distributions all over the world (Thomas et al. 2004). One of the main advantages of NB models is their relative simplicity, facilitating development of many species-specific models so long as reliable distributional data are available. One of the main criticisms of NB models, however, is their failure to consider relationships such as biotic interactions, mortality, or growth (Davis et al. 1998, Hampe 2004) and their reliance on observed distributions, which are the results of long-term historical factors (e.g., post-glacial recolonization), biotic interactions, and environmental stochasticity, among others factors.

Species-specific, process-based (PB) models on the other hand do predict the response of an individual or a population to environmental conditions by explicitly incorporating biological processes calibrated with observations on individuals in natural populations. These PB models can predict abundance, cover, or probability of presence of a species at a given location, and they can take genetic or ecotypic variability into account when observations are available for different individuals or different populations of a species (e.g., Morin et al. 2007). A PB model allows the highlighting of processes involved in range shifts or extinction. Although various types of PB models are developed or are under development, such as gap models (Pacala et al. 1993, Bugmann 2001), landscape models (Higgins et al. 2000, Lischke et al. 2006, Scheller et al. 2007), or fitness-based models (Chuine and Beaubien 2001), the use of these models to make predictions of species range shifts is still rare (Schumacher et al. 2004, Scheller and Mladenoff 2005), especially for species ranges at the continental scale (Hijmans and Graham 2006, Jeltsch et al. 2008). This scarcity in the number of species for which we dispose of relevant and calibrated PB models is caused by the fact that they require a large amount of knowledge and data to be calibrated. These applications are thus restricted to well-known species for which demography or physiology have been studied for a long time. This important limitation has so far prevented the use of such models to assess the impact of climate change on biodiversity (Jeltsch et al. 2008).

Despite their broad use, uncertainties about NB models predictions remain high (Loehle and LeBlanc 1996, Bolliger et al. 2000, Hampe 2004, Thuiller et al. 2004, Randin et al. 2006), and there have been very few opportunities to compare NB predictions against other modeling approaches because relatively few species-specific PB models have been developed at the continental scale (but see Hijmans and Graham 2006). However, as with climatic models (or any other predictive models), it is important to develop several models independently and to compare and contrast their predictions in order to identify both robust results and model inadequacies (Beaumont et al. 2007). Such cross-comparisons may provide conclusions on which policy makers and stakeholders can rely. It is therefore critical at this time that NB and PB models be developed and compared for the same species run under the same

scenarios. Toward this end, in this paper we address two questions: Do the simulations made with species distributions models relying on different assumptions show consistent results for the future? And if not, what can we learn from these differences in relationship with the assumptions of each model?

Because NB and PB models focus on different aspects of species performance across environments, there are real insights to be gained in such a comparison. The species-specific PB models at continental scale (Chuine and Beaubien 2001, Hijmans and Graham 2006) rely on modeling the fundamental niche of species, i.e., the niche defined by only abiotic environmental variables under which individuals of a species can live and reproduce without any limitation by biotic interactions (Hutchinson 1957, Pulliam 2000). Competitive and facilitative processes at both intra- and interspecific levels are thus excluded. The NB models in contrast rely on modeling the distribution realized in the face of biotic factors, land use legacy, and dispersal abilities that restrict the geographic expression of the fundamental niche, i.e., the realized niche (Pulliam 2000). In this way, they do not explicitly model abiotic stress and biotic interactions that drive species distribution, but they integrate the a posteriori outcome of every potential constraint on the geographic distribution of species. As they rely on different assumptions, the natural complementarity of PB and NB models can be exploited to provide a more accurate picture of species future distributions (Midgley and Thuiller 2005, Midgley et al. 2007) through the comparison of both kinds of models.

At the continental scale of this study, we can expect that PB models predictions will be more conservative (i.e., will predict weaker range shifts than NB models) as they simulate the geographic expression of the fundamental niche. But should this hypothesis be true, how large will this difference be? Will it be consistent across species? Where will the zones showing similar predictions with both models be located? Comparing predictions for models of each kind, and in particular highlighting the areas sharing the same predictions, is certainly a relevant way to reduce prediction uncertainty. Following this idea, we here compare predictions of range shifts under climate change scenarios for a NB model with those for a PB model for 15 North American boreal and temperate tree species.

## METHODS

### Choice of the species distribution models

For each of 15 northeastern American tree species (Table 1), we simulated current and future distribution using (1) a process-based model and (2) an ensemble of niche-based models. Using more models of each kind (NB and PB) would have been valuable, but we chose to focus on one type of model of each kind. In fact we should note that the framework we used, Biomod, with few exceptions, calibrates the most well-known and well-developed NB models. Thus the predictions made with this framework will be consistent with several common models and can be seen as an ensemble of the most reliable models. More generally, NB models share the same philosophy (i.e., assessing the geographic realization of the realized niche by relating observed distribution and environmental variables) and just differ in the kind of statistical relationships they use to do so.

Regarding PB models, actually very few models working at both the tree species level and the continental scale exist. For temperate trees, although new developments might lead to promising perspectives soon (see *Introduction*, as well as Morin et al. 2008), the PB model we used, Phenofit, is the only model developed so far at such a level and such a scale.

### The PB model: Phenofit

The process-based model Phenofit (Chuine and Beaubien 2001, Morin and Chuine 2005, Morin et al. 2007) is so far one of the only process-based models that predicts temperate tree species distributions at the continental scale. It relies on the principle that the adaptation of a tree species to environmental conditions depends on the synchronization of its timing of development to the seasonal variations of climate. Thus Phenofit outputs a mean probability of presence in a given location by assessing the fitness of an adult tree of the studied species after several years. It is noteworthy that most PB models are based on carbon–water balance and focus on modeling growth of individuals (Sitch et al. 2003, Hijmans and Graham 2006), while Phenofit focuses instead on the impact of stress limits on fitness. To do so, this "fitness-based model" focuses on the ability of trees to survive until the next reproductive season and to produce viable seeds before the end of the annual cycle (reproductive success). Appendix A provides a detailed description of the model. By using sets of parameters fitted to observations on different populations, the model can take into account the genetic differentiation among populations and local adaptation to climate (Morin et al. 2007). For five of the 15 species studied (*Acer saccharum*, *Fraxinus americana*, *Populus tremuloides*, *Quercus macrocarpa*, and *Ulmus americana*), parameter sets were available for two different populations, one from northern Ohio and another from central Illinois. For these five species Phenofit was run with each set of parameters separately, and the results of each simulation were combined using a squared inverse-distance correction. The validation of Phenofit for the 15 species studied here is detailed in Morin et al. (2007).

One of these 15 species (quaking aspen, *Populus tremuloides*) is known to significantly propagate with vegetative reproduction (Russell et al. 1990). Asexual reproduction is not taken into account in Phenofit, which may affect the quality of the predictions for this species. In a range shift context due to climate change, vegetative reproduction may be important in two situations: colonizations at the leading edge of the expanding range and local extinctions of populations at

TABLE 1. Species-specific percentages of extinctions and range extension (with and without migration [Mig] limitation) under the climate scenarios A2 and B2, for niched-based (NB) and process-based (PB) simulations.

| Species | $r$ (km/yr) | A2 | | | | | | B2 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Loss NB | Loss PB | Gain NB | Gain PB | Mig NB | Mig PB | Loss NB | Loss PB | Gain NB | Gain PB | Mig NB | Mig PB |
| Group 1 | | | | | | | | | | | | | |
| *Acer saccharinum* | 1 | 45.0 | 16.4 | 89.3 | 98.0 | 19.0 | 14.1 | 42.0 | 10.7 | 71.5 | 87.7 | 18.9 | 13.4 |
| *Acer saccharum* | 1 | 54.0 | 5.1 | 89.7 | 122.5 | 12.6 | 18.4 | 53.9 | 10.6 | 65.3 | 109.7 | 12.8 | 19.2 |
| *Carya ovata* | 1 | 39.5 | 21.4 | 84.7 | 85.2 | 17.1 | 15.4 | 34.1 | 28.1 | 63.0 | 88.2 | 18.0 | 14.8 |
| *Juglans nigra* | 1 | 38.6 | 11.4 | 84.3 | 56.3 | 16.9 | 11.6 | 34.0 | 9.0 | 62.1 | 66.2 | 17.8 | 14.7 |
| *Ostrya virginiana* | 1 | 23.8 | 13.2 | 89.0 | 64.8 | 15.2 | 8.9 | 28.7 | 18.2 | 61.7 | 62.5 | 15.1 | 11.1 |
| *Populus deltoides* | 10 | 24.0 | 5.5 | 89.9 | 62.3 | 89.9 | 30.8 | 22.0 | 4.0 | 64.1 | 27.6 | 64.1 | 27.6 |
| *Populus tremuloides* | 10 | 27.4 | 4.1 | 31.3 | 46.9 | 31.3 | 32.1 | 20.4 | 4.8 | 27.1 | 38.9 | 27.1 | 29.7 |
| *Quercus bicolor* | 1 | 91.3 | 30.3 | 164.3 | 124.0 | 27.9 | 14.4 | 73.7 | 31.5 | 111.6 | 106.2 | 32.2 | 14.6 |
| *Quercus macrocarpa* | 1 | 24.9 | 18.4 | 162.5 | 92.4 | 28.8 | 10.2 | 26.7 | 17.2 | 120.9 | 75.5 | 27.5 | 11.6 |
| *Ulmus americana* | 4 | 17.0 | 2.5 | 70.8 | 112.5 | 49.0 | 25.7 | 15.3 | 4.1 | 55.6 | 94.5 | 41.4 | 23.7 |
| Mean | | 38.6 | 12.8 | 95.6 | 86.5 | 30.8 | 18.2 | 35.1 | 13.8 | 70.3 | 75.7 | 27.5 | 18.0 |
| SE | | 6.9 | 2.8 | 12.6 | 8.9 | 7.4 | 2.7 | 5.6 | 3.1 | 8.6 | 8.6 | 4.9 | 2.1 |
| Group 2 | | | | | | | | | | | | | |
| *Fraxinus americana* | 1 | 11.0 | 60.1 | 64.0 | 60.3 | 17.5 | 17.5 | 13.0 | 12.8 | 52.1 | 112.7 | 16.8 | 22.3 |
| *Fraxinus nigra* | 1 | 55.0 | 97.4 | 110.7 | 54.0 | 15.8 | 4.4 | 46.2 | 98.2 | 79.8 | 48.2 | 16.2 | 4.0 |
| Mean | | 33.0 | 78.8 | 87.3 | 57.2 | 16.7 | 11.0 | 29.6 | 55.5 | 65.9 | 80.5 | 16.5 | 13.1 |
| SE | | 22.0 | 18.6 | 23.4 | 3.1 | 0.9 | 6.6 | 16.6 | 42.7 | 13.9 | 32.3 | 0.3 | 9.1 |
| Group 3 | | | | | | | | | | | | | |
| *Aesculus glabra* | 1 | 19.0 | 29.4 | 119.1 | 57.6 | 30.4 | 9.7 | 33.6 | 16.4 | 77.9 | 57.9 | 23.9 | 11.5 |
| *Salix nigra* | 5 | 5.2 | 2.9 | 125.7 | 61.1 | 112.4 | 38.6 | 3.6 | 9.3 | 97.0 | 50.7 | 95.0 | 31.0 |
| *Sassafras albidum* | 1 | 22.1 | 20.0 | 56.2 | 34.3 | 13.8 | 6.0 | 13.6 | 10.5 | 47.9 | 29.4 | 16.1 | 5.4 |
| Mean | | 15.4 | 17.5 | 100.4 | 51.0 | 52.2 | 18.1 | 16.9 | 12.1 | 74.3 | 46.0 | 45.0 | 16.0 |
| SE | | 5.2 | 7.8 | 22.2 | 8.4 | 30.5 | 10.3 | 8.8 | 2.2 | 14.3 | 8.6 | 25.1 | 7.7 |

*Notes:* The species have been gathered according to the groups identified (see *Results*): Group 1, species for which the proportion of extinctions (in percentages of the number of pixels included in the species distribution in 2000) in NB simulations exceeds the one in PB simulations; Group 2, species for which the proportion of extinctions in PB simulations exceeds the one in NB simulations; Group 3, species for which differences in extinctions between NB and PB simulations are small. Specific dispersal rate ($r$), percentages of extinctions in 2100 for NB (Loss NB) and PB (Loss PB) models, percentages of pixels colonized in 2100 for NB (Gain NB) and PB (Gain PB) models, and percentages of pixels colonized in 2100 by taking migration limitation into account for NB (Mig NB) and PB (Mig PB) models are shown. Means are averaged values for all species. In each case the change (in percentage) in range size has been calculated in reference to simulated range size in 2000. Explanations for the climate scenarios A2 and B2 can be found in *Methods: Climate data*.

the trailing edge. At the leading edge, vegetative reproduction can allow the dissemination of the species in areas not suitable for sexual reproduction, although the rate of colonization by clonal reproduction is negligible compared to sexual reproduction (e.g., Rice and Sax 2005). At the trailing edge, vegetative reproduction might allow persistence of populations under new conditions adverse to sexual reproduction, but vegetative re-sprouts also may well be as sensitive to frost and drought damage as seedlings. Thus, although the Phenofit predictions for colonization events by quaking aspen should be taken with some caution at local spatial scales, we can expect Phenofit predictions for this species at the continental scale to be reasonably accurate. This statement is strengthened by the high consistency between Phenofit simulations and the presently observed distribution of *Populus tremuloides* (Chuine and Beaubien 2001, Morin et al. 2007).

### The NB model: the Biomod framework

We calibrated and evaluated NB models using the Biomod framework (see details in Thuiller 2003, 2004,

Thuiller et al. 2008*b*) under the R software (Ihaka and Gentleman 1996). Biomod enables many NB models to be run simultaneously on a large suite of species and for an unlimited number of climate change scenarios. Models include: (1) generalized linear models (GLM), (2) generalized additive models (GAM), (3) classification tree analysis (CTA), (4) feed-forward artificial neural networks (ANN), (5) generalized boosting models (GBM; also known as boosting regression trees; BRT), (6) random forests (RF), (7) mixture discriminant analysis (MDA), and (8) multivariate adaptive regression spline (MARS). Generalized linear models, GAM, CTA, and ANN are described and discussed in Thuiller (2003). In a recent test of 16 niche models (Elith et al. 2006), including GBM, MARS, GLM, GAM and CTA, the GBM models performed best. For each species, five models were calibrated: GLM, GAM, CTA, Random-Forest, and GBM and then an ensemble approach was followed.

To evaluate the quality of NB predictions, we divided the available data into two subsets: one for calibration and the other for evaluation. We first calibrated the

models using a random subsample of data (70%) relating distributions of our 15 study species to six climate variables: growing degree days above 5.5°C, mean annual precipitation, summer precipitation, winter precipitation, minimum temperature of the coldest month, and potential evapotranspiration calculated using the Food and Agricultural Organization (FAO) 56 Penman Monteith combination equation (Allen et al. 1998). For each species, each of the five models was then evaluated on the remaining 30% of the initial data set. Model accuracy was calculated using the values obtained from the area under the curve (AUC) of a receiver operating characteristic (ROC) plot of sensitivity against 1 − specificity following Swets (1988). Sensitivity is defined as the proportion of true positives correctly predicted across all cells (pixels) in the range, whereas specificity is the proportion of true negatives correctly predicted (Fielding and Bell 1997). For each species the five models were ranked according to the AUC values, and only the best three simulations (i.e., from the best three models) conserved. Their rank order was scored 3, 2, or 1, which were then standardized to produce a vector of weights whose elements sum to unity. Final projections are a weighted average of these three best simulations for each of our 15 study species (Hartley et al. 2006; Marmion et al., *in press*). We then transformed the probability of occurrence (continuous values) into presence/absence (binary values) using a threshold maximizing the percentage of presence and absence correctly predicted (Pearce and Ferrier 2000). For these NB simulations, the final accuracy of the simulations was assessed using ROC curves (Thuiller 2003).

### Climate data

To simulate the initial distribution of the species, we used the CRU TS 2.0 data set (Climatic Research Unit, University of East Anglia, UK [New et al. 2000]). This data set consists of monthly mean and minimal temperature and monthly precipitation for the 20th century (1901–2000) at a 0.5° × 0.5° grid resolution. These data were obtained by interpolation of observed climatic data for >20 000 weather stations around the world (New et al. 2000). The variables required by the NB models have been directly derived from these data. As the performance of the PB model was greatly affected by the temporal resolution of data (Morin and Chuine 2005), we generated daily data (for mean and minimum temperatures) following the classical method used by weather generators, e.g., Cligen (Nicks et al. 1995). The PB model was run using these daily variables. For further details see Morin and Chuine (2005) and Morin et al. (2007).

To simulate the future distribution of species, we used data from the HadCM3 GCM (Hadley Center for Climate Predictions and Research, UK [Pope et al. 2000]) for the period 2001–2100. We used two Intergovernmental Panel on Climate Change (IPCC) story lines, A2 and B2 (IPCC 2001). These two scenarios were

chosen because they describe contrasted climatic conditions for the next century. The aim of the study was not to compare range shifts across a large number of scenarios but to highlight whether there might be some specific difference across two contrasting scenarios. The A2 story line describes a global increase of mean temperature of 3.2°C on average over North America in 2100. The B2 story line describes a global increase of mean temperature of 1.0°C on average over North America in 2100. For the PB model we used HadCM3 daily data for mean and minimum temperatures (provided by the LINK Project; *available online*),[5] while for the NB models we used monthly averages of these data. To keep consistency in spatial resolution, the HadCM3 data (resolution of 3.75° × 2.5°) were disaggregated at the CRU TS 2.0 data set resolution (i.e., 0.5° × 0.5°) with an elevation adjustment (Morin and Chuine 2005).

### Simulations

For Phenofit simulations (the PB model), the initial distribution of each of the 15 tree species (i.e., current range) was the distribution simulated by the model at the end of the 20th century (in 2000) using daily climatic data generated from the CRU TS 2.0 data set for a 0.5° × 0.5° grid resolution (Morin et al. 2007). Because Phenofit works at a yearly time step, its predictions are better if performed on a large number of years, to minimize the effect of years with extreme values. Thus the modeling of current distributions using Phenofit was made with a 100-year period. The NB simulations of the initial distribution of the species were performed using monthly date from the CRU TS 2.0 data set for 1960–2000.

For both kinds of models, we then simulated the species distribution for the 21st century using the A2 and B2 story lines from the HadCM3 GCM data. The NB model simulations were made using monthly normals for the period 2060–2100. The Phenofit simulations were made using daily climatic data between 2001 and 2100 (Morin et al. 2008). For each species, the presence predicted by Phenofit in each pixel is updated annually. This constraint requires keeping temporal continuity between the two data sets (i.e., current and future climatic conditions), which explains why the Phenofit simulations have been made for 2001–2100. The last years of simulation, which drive the final presence or absence of species, are the same as those used in NB predictions (2060–2100); this is the key point allowing meaningful comparison of the two kinds of models.

To consider migration processes, we used specific migration rate estimates from paleoecological studies on the last glaciation–deglaciation cycle between 18 000 and 6000 yr before present (BP; Davis 1976, Huntley and Birks 1983), as in Morin et al. (2008). These estimates integrate species dispersal ability including long-distance

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[5] ⟨http://badc.nerc.ac.uk/data/link/⟩

dispersal events and establishment success probability. Migration rates vary from 1 to 10 km/yr according to the species (Table 1). A grid cell in which the species is not present could be colonized only if the cell were both (1) reachable and (2) climatically suitable for the establishment and survival of the species. (1) An empty cell (a sink cell) was reachable if it was next to at least one cell where the species is present (a source cell). (2) A sink cell was colonizable if the predicted probability of presence was superior or equal to a species-specific probability of presence, calculated in Morin et al. (2007). A newly colonized cell can become a source cell only if the probability of presence is superior or equal to the specific probability of presence during a specific number of years $s$, which depends on the species migration rate $r$ (in kilometers per year) as follows:

$$s = \frac{55}{r}$$

where 55 km is the length of a cell of 0.5° latitude × 0.5° longitude.

Note that at the beginning of the simulation (i.e., in 2000), grid cells in which the species was present were all defined as sources. Local extinction in a cell occurred when the simulated probability of presence was inferior to the specific probability of presence.

We constrained the migration of the species using the migration rate estimates on the last glaciation-deglaciation cycle, even if the climate becomes suitable at greater distances than can be reached by dispersal in a given time period. For instance, a species with a migration rate of only 1 km/yr effectively restricts species movement to a maximum of 0.5° for the 50-year period until 2050 or 1° for the 100-year period. Any pixel geographically beyond these dispersal limits for a given species was assigned a probability of occurrence equal to zero even if the climate at that pixel was suitable for the species.

The paleoecological migration rates we used in these simulations may not represent maximal rates because during deglaciation species may have been limited first by the progress of the warming northward, not by their dispersal ability (Huntley 1991). As the present rate of warming is unparalleled in the Quaternary (Huntley 1991, Higgins et al. 2003), the actual migration rate might be larger than those we used. Nevertheless, we will consider the rates we used as among the largest possible.

### Comparisons of models predictions

For each species, we compared the predictions of the NB and PB models. More precisely, we compared, for each species (1) the percentage of sites (i.e., pixels) of the current distribution (in 2000) where a given species is predicted to go extinct in 2100; (2) the proportion of sites newly suitable in 2100 (quantified from the area of the current distribution in 2000); and (3) the proportion of sites newly suitable in 2100 predicted to be truly colonized under migration limitations. Note that as NB

and PB simulations of current distributions necessarily differ, at least slightly, we have only calculated the proportion of "shared extinctions" from the sites predicted to be in a species' range by both kinds of models.

## RESULTS

### Niche-based and process-based models' accuracy

For the current species ranges, the AUC values of the NB simulations ranged from 0.85 to 0.99 (mean = 0.96). The AUC values of the PB simulations ranged from 0.87 to 0.98 (mean = 0.94) (Morin et al. 2007). These values of AUC mean that both models showed high levels of accuracy according to Swets (1988).

### Comparisons of niche and process-based predictions

*Extinctions.*—Species fall into three groups according to the average of the two scenario simulations for each species (Fig. 1 and Appendix B): (1) species for which the proportion of extinctions in NB simulations exceeds that in PB simulations (*Acer saccharinum*, *Acer saccharum*, *Carya ovata*, *Juglans nigra*, *Ostrya virginiana*, *Populus deltoides*, *Populus tremuloides*, *Quercus bicolor*, *Quercus macrocarpa*, *Ulmus americana*); (2) species for which the proportion of extinctions in PB simulations exceeds that in NB simulations (*Fraxinus americana*, *Fraxinus nigra*); and (3) species for which differences in proportion of extinctions between NB and PB simulations are small (i.e., fewer than five points; *Aesculus glabra*, *Salix nigra*, *Sassafras albidum*). On average 85.3% of 30 simulations (15 species, two scenarios) predicted a lower proportion of extinctions with the PB model than with the NB model (Table 1, Fig. 2). For scenario A2, only *A. glabra*, *F. americana*, and *F. nigra* had a percentage extinction greater with the PB model. For scenario B2, this was only the case for *F. nigra* and *S. nigra* (Table 1, Fig. 2).

The mean proportion of extinctions is ~50% higher in NB predictions (33.2 vs. 22.6, respectively, for NB vs. PB simulations in scenario A2; 30.7 vs. 19.0, respectively, for NB vs. PB simulations in scenario B2; Table 1). Furthermore, the sites where species are predicted to go extinct in 2100 are not necessarily the same in the two kinds of simulations. Only 26% (for A2) and 15% (for B2) of the sites experiencing species extinction according to NB simulations are also predicted to experience species extinctions with the PB simulations (Table 2). This result is not surprising as the mean proportion of extinctions is higher in NB predictions, and one potential explanation may be that the sites where the PB model predicted species extinctions are on average a subsample of the niche-based predicted extinctions sites (Fig. 1). However only 62% (for A2) and 45% (for B2) of the sites experiencing species extinction according to PB simulations are also predicted to experience species extinction with the NB simulations (Table 2). Thus the sites experiencing species extinctions clearly differ according to the kind of model (Fig. 1 and Appendix
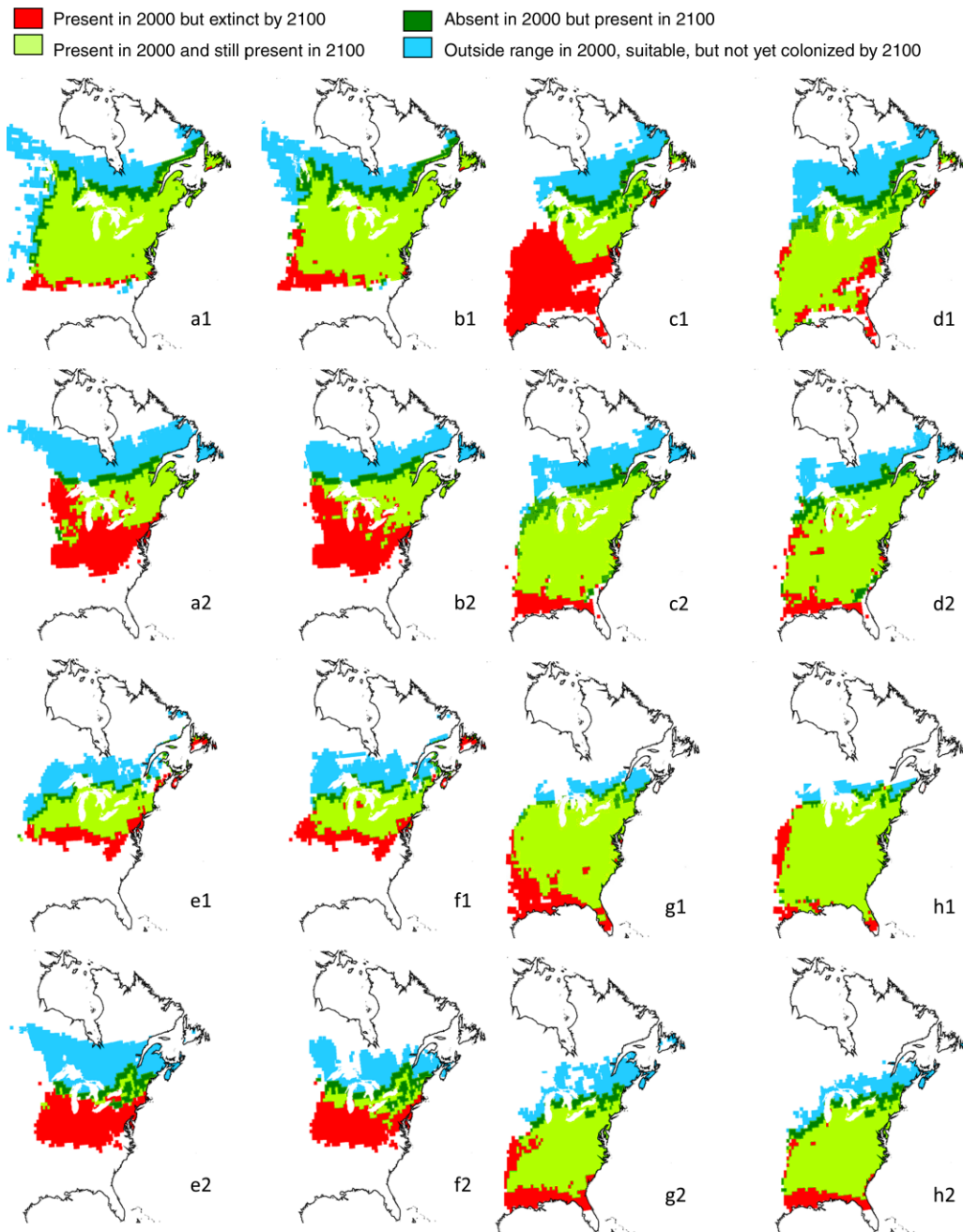
FIG. 1. Comparisons between species probability of presence in 2100 with species probability of presence in 2000 made with process-based (PB) and an ensemble of niche-based (NB) models for four species: *Acer saccharum* (PB, a1–b1; NB, a2–b2); *Fraxinus americana* (PB, c1–d1; NB, c2–d2); *Quercus bicolor* (PB, e1–f1; NB, e2–f2); *Sassafras albidum* (PB, g1–h1; NB, g2–h2). The right figure in each pair represents the results based on the Intergovernmental Panel on Climate Change (IPCC) scenario A2, and the left represents the results based on the IPCC scenario B2. Explanations for the climate scenarios A2 and B2 can be found in *Methods: Climate data.*

B). We have also calculated the percentage of overlap in predicted extinctions between the two kinds of simulations in each group. It appears that the overlap is weak for the group 1 (21.9% ± 6.4% [mean ± SE]) and larger for two other groups, although still lower than 50% (48.3% ± 1.8%).

*Colonizations and migration limitation.*—The proportion of predicted newly suitable habitats is larger with the NB predictions, especially under scenario A2 (Table 1). However, for both kinds of simulations, the colonization is strongly limited by migration (Table 1, Fig. 1). In NB simulations, species may reach on average
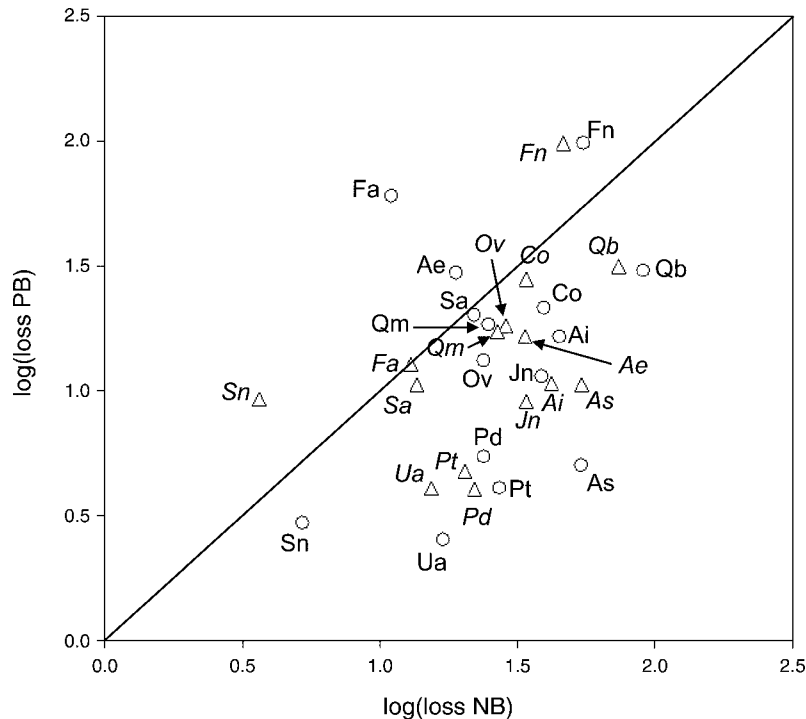
Fig. 2. Log(percentage of extinction) from the process-based (PB) prediction (*y*-axis) vs. log(percentage of extinction) from the niche-based (NB) prediction (*x*-axis) for the 15 species, shown separately for the Intergovernmental Panel on Climate Change (IPCC) scenarios A2 (circles and regular type) and B2 (triangles and italic type). Species abbreviations are: Ai, *Acer saccharinum*; As, *Acer saccharum*; Ae, *Aesculus glabra*; Co, *Carya ovata*; Fa, *Fraxinus americana*; Fn, *Fraxinus nigra*; Jn, *Juglans nigra*; Ov, *Ostrya virginiana*; Pd, *Populus deltoides*; Pt, *Populus tremuloides*; Qb, *Quercus bicolor*; Qm, *Quercus macrocarpa*; Sn, *Salix nigra*; Sa, *Sassafras albidum*; Ua, *Ulmus americana*. Explanations for the climate scenarios A2 and B2 can be found in *Methods: Climate data*.

~35% of their newly suitable habitats under scenario A2 and 42% under scenario B2. These percentages are even weaker for PB simulations: on average species are predicted to colonize only 23% of the newly suitable habitats under scenario A2 and 24% under scenario B2.

### DISCUSSION

There is considerable recent interest in the issue of consistency in predictions from different modeling approaches to questions of plant distribution under future climate regimes. A number of recent studies using several different projections of niche-based models (Araujo et al. 2006, Hartley et al. 2006, Araujo and New 2007, Thuiller 2007) have shown the value of ensemble forecasting of range shifts under climate change. Hijmans and Graham (2006) further considered comparisons of qualitatively different modeling approaches, in particular comparing predictions from a climatic envelope model and a mechanistic model for crop species in the Americas. Their extension of the discussion to substantially different modeling approaches is an important advance, but their unvalidated submodels were fairly simplistic and applied to controlled agricultural environments where competitive interactions are minimal. In recent years, NB models have predicted that the geographic realization of the

climatic niche will be shifted polewards and toward higher elevation for many species (e.g., Thomas et al. 2004). To extend these initial inquiries we undertook a comprehensive comparison of simulations for distributions of forest tree species using both process-based and niche-based models for the next century. Our study is essentially a proof of concept comparison made using a single PB model and a NB modeling framework designed to illustrate the importance of combining outputs from complementary modeling approaches. Although focused on a modest number of tree species, our comparison of the predictions from the PB model Phenofit with those from an ensemble of NB models has shown that alarming predictions about extinctions due to climate change should be tempered despite the fact that species may have trouble tracking their climatic niche because of migration constraints. We elaborate these points in the following discussion.

### Similar predicted trends across models

From a qualitative point of view, both PB and NB models predict that tree species' ranges will be shifted polewards, and for most species, this shift will be strongly constrained by dispersal ability, while local extinctions will occur in the south of the species range. For both kinds of models, we observed an interesting

TABLE 2.   Species-specific percentages of pixels experiencing species' extinction in the niche-based (NB) and the process-based (PB) simulations, under the climate scenarios A2 and B2.

| Species | r | A2 %NB | A2 %PB | B2 %NB | B2 %PB |
|---|---|---|---|---|---|
| Group 1 | | | | | |
| *Acer saccharinum* | 1 | 13.2 | 79.7 | 4.8 | 100.0 |
| *Acer saccharum* | 1 | 1.3 | 100.0 | 1.1 | 24.0 |
| *Carya ovata* | 1 | 22.8 | 71.8 | 20.8 | 34.9 |
| *Juglans nigra* | 1 | 5.3 | 94.4 | 0.0 | 0.0 |
| *Ostrya virginiana* | 1 | 7.8 | 16.3 | 4.6 | 8.4 |
| *Populus deltoides* | 10 | 10.6 | 51.9 | 7.0 | 42.1 |
| *Populus tremuloides* | 10 | 0.5 | 100.0 | 0.7 | 100.0 |
| *Quercus bicolor* | 1 | 31.3 | 100.0 | 33.1 | 94.8 |
| *Quercus macrocarpa* | 1 | 31.0 | 61.5 | 11.8 | 27.9 |
| *Ulmus americana* | 4 | 3.4 | 86.7 | 3.8 | 46.4 |
| Mean | | 12.7 | 76.2 | 8.8 | 47.9 |
| SE | | 3.7 | 8.5 | 3.3 | 11.9 |
| Group 2 | | | | | |
| *Fraxinus americana* | 1 | 68.1 | 12.8 | 12.1 | 16.8 |
| *Fraxinus nigra* | 1 | 96.0 | 56.3 | 93.5 | 44.4 |
| Mean | | 82.0 | 34.5 | 52.8 | 30.6 |
| SE | | 14.0 | 21.7 | 40.7 | 13.8 |
| Group 3 | | | | | |
| *Aesculus glabra* | 1 | 40.8 | 26.0 | 16.2 | 53.3 |
| *Salix nigra* | 5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Sassafras albidum* | 1 | 57.2 | 66.9 | 16.5 | 85.0 |
| Mean | | 32.7 | 31.0 | 10.9 | 46.1 |
| SE | | 17.0 | 19.5 | 5.4 | 24.8 |

*Notes:* Species-specific percentage of pixels experiencing species extinction in 2100 by the NB model that are also predicted to experience species' extinction by the PB model (%NB) and species-specific percentage of pixels experiencing species' extinction in 2100 by the PB model that are also predicted to experience species' extinction by the NB model (%PB) are shown. For instance, for *Acer saccharinum*, under scenario A2, 13% of the pixels experiencing species extinction in 2100 by the NB simulation are also predicted to experience species extinction by the PB simulation, while 79% of the pixels experiencing species extinction in 2100 by the PB simulation are also predicted to experience species extinction by the NB simulation. Groups are as in Table 1. Explanations for the climate scenarios A2 and B2 can be found in *Methods: Climate data.*

broad trend among the tested species: species with an early phenology and light seeds (e.g., *Salix nigra*, *Ulmus americana*, *Populus deltoides*, *Populus tremuloides*) exhibit less risk of extinction, while species with later phenology and heavier seeds (e.g., *Quercus bicolor*, *Carya ovata*, *Acer saccharum*) have a greater risk (Fig. 2). Furthermore the number of sites where a given species is predicted to go extinct in 2100 in both simulations is negatively correlated to the species range size ($r = -0.44$ for A2 and $r = -0.42$ for B2, Pearson's correlations, log-transformed data). Thus the species-specific "common sensitivity" to extinction (i.e., regarding the two kinds of models) appears to be stronger for narrowly distributed species.

### Differences between predictions from the two types of models

From a quantitative point of view, our results show clearly that predictions, made for the same set of species and using the same raw data, can differ according to the kind of model used. Although the results are very species-specific, two general patterns emerged. First, the ensemble of niche-based models tended to predict a higher level of extinction in comparison with the process-based model. The only species showing an opposite trend is *Fraxinus nigra*, a species among the most sensitive to frost in the latitudinal range we studied. Second, the NB predictions also showed a greater proportion of colonized sites compared to the PB model. What might underlie these different simulation outcomes?

First, the two kinds of models do not rely on the same assumptions. The NB models all simulate the distribution of a species from distributional data in nature that represent the realized niche (Hutchinson 1957, Pulliam 2000) for the species. Phenofit, on the other hand, predicts a distribution using only data on ecophysiological responses to abiotic variables that determine the fundamental niche of species. A previous study has shown that at the continental scale, the "potential distribution" (i.e., the geographic area defined by the fundamental niche) seems to accurately fit the observed distribution for most of the species studied here (Morin et al. 2007). We can suppose that a climatic envelope based on the realized niche imposes greater constraints for a species under climate change than a model based

on the fundamental niche, although there is no clear evidence to that effect. Second, we might argue that ecophysiological control systems respond to climatic interannual variations to generate observed year-to-year phenological variation. The NB models are built on generalized climate–distribution correlations and cannot take account of variation due to the day-to-day progression in meteorological conditions from year to year (Hampe 2004, Randin et al. 2006). In contrast, a PB model such as Phenofit is designed specifically to quantify these effects by describing several processes controlling phenology as nonlinear functions of daily temperature progressions. This sort of interannual variation in phenology is especially important in adaptive traits triggered by climate (Rathcke and Lacey 1985) and may be crucial in determining individual responses to climate change (Jump and Penuelas 2005).

However, although NB models predict a more drastic level of extinction, the predictions from the two types of models can be considered complementary because the models rely on different assumptions. We can consider their predictions independent, although carried out for the same climatic scenarios. When the model predictions converge, the reliability of the predictions is greater. For example, we expect that a site (pixel) predicted to experience species extinction in 2100 in both simulations can be considered a very sensitive zone for the considered species. Such comparisons between the predictions of models built using different approaches provide an effective way to compensate for prediction uncertainties (Beaumont et al. 2007).

### Migration

The predictions of both kinds of models raised migration as a crucial issue (see Thuiller et al. 2008a for a review). This result was observed as we used "optimistic" migration rates, i.e., upper limit of migration rates estimated by paleoecological studies (Huntley and Birks 1983). Even if potential migration rates are actually higher than the ones in our simulations, realized migration rates may also be limited by habitat fragmentation caused by human activities (Honnay et al. 2002, Travis 2003). In coming decades colonizing individuals will have to colonize both fragmented and established forests (i.e., high competition levels), which was not the case during the recolonization phase at the end of the last glaciation period, and this may slow migration northwards. On the other hand, recent studies in invasion ecology have shown that propagule pressure and residence time are crucial parameters determining spread rate (Lockwood et al. 2005, Richardson and Pysek 2006, Wilson et al. 2007), which implies that direct human intervention in dispersal through seeding or transplanting of stock could increase the effective rates of range expansion.

The predicted range shifts from models in the last 15 years are so great that many authors have questioned whether species will be able to migrate fast enough to track their climatic niche (Malcolm et al. 2002, Higgins et al. 2003, Midgley et al. 2007), but a precise estimate of the time lag between climate shift and species range shift has rarely been assessed (but see Dullinger et al. 2004). At the continental scale, very few predictions have been made incorporating migration rates, and these studies were only performed using NB models (Iverson et al. 2004, Broennimann et al. 2006, Midgley et al. 2006). Iverson et al. (2004) predicted limited realized range shifts of species due to migration limitations and that very long but rare distance migration events are not sufficient to rescue migration. The next step toward better predictions in models of species range under climate change is to take migration processes explicitly into account (Neilson et al. 2005, Midgley et al. 2007, Thuiller et al. 2008a). This will require downscaling the spatial structure of models, an effort that has been begun at a landscape/regional scale using simple, process-based rules for seed dispersal and seedling establishment (Scheller and Mladenoff 2005). There are encouraging signs that it will be possible to refine continental-scale predictions to local spatial scale by coupling different models (Midgley et al. 2007, Thuiller et al. 2008a).

### Toward a hybrid cross-scaling model

The need for "hybrid" models has been invoked to better assess the fate of propagules at the leading edge of species distributions under climate change (Midgley et al. 2007). Trying to achieve a compromise between realism and accuracy, these models basically incorporate different submodels working at different spatial scales (Thuiller et al. 2008a). Previous attempts mostly relied on the prediction of presence according to growth functions (Smith et al. 2001, Lischke et al. 2006). The fact that Phenofit deals with the fundamental niche while NB models deal with the realized niche highlights their possible complementarity and opens a new way to build a hybrid model. Similar approaches mixing PFT model predictions with species bioclimatic envelopes have been attempted (Koca et al. 2006). Like other hybrid projects, a crucial problem in obtaining reliable predictions at finer spatial scales is the modeling of migration and recruitment (see Thuiller et al. 2008a). Current advances provide encouraging developments in this regard through Bayesian approaches (Wikle 2003) and through the increasing understanding of long-distance dispersal processes (Nathan 2006).

### CONCLUSION

Despite the increasing number of articles assessing the impacts of climate change on species distributions over the last 10 years, there have been very few quantitative comparisons between the two tools of choice: niche-based and process-based models. Besides the inherent differences between the concepts, philosophies, and main results of the two approaches, this quantitative comparison revealed several key points. (1) Process-

based models, focusing largely on the modeling of fundamental niches, are less pessimistic than niche-based models, which focus on the realized niche of the species and are thus an incomplete representation of the true physiological limits. (2) Using both approaches in concert, each with its own caveats and advantages, is crucial to achieve robust predictions. In the future, more efforts should be made to compare different approaches, an exciting challenge that can yield more reliable predictions about the fates of species. (3) Alarming predictions about extinction rates should probably be tempered, at least in the short term (the next decades), for long-lived dominant species. (4) Migration is the key driver of the survival of species in particular regions. A crucial challenge is thus to deal with migration spatially and mechanistically, which requires building more complex hybrid models.

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## APPENDIX A

Description of the model Phenofit (*Ecological Archives* E090-085-A1).

## APPENDIX B

Comparisons between species probability of presence in 2100 with species probability of presence in 2000 made with process-based (PB) and an ensemble of niche-based (NB) models for the 11 other species (*Ecological Archives* E090-085-A2).