CLIMATE CHANGE CAN CAUSE SPATIAL MISMATCH OF TROPHICALLY INTERACTING SPECIES

Oliver Schweiger,[1,2,4] Josef Settele,[1] Otakar Kudrna,[3] Stefan Klotz,[1,2] and Ingolf Kühn[1,2]

[1]*Helmholtz Centre for Environmental Research—UFZ, Department of Community Ecology,
Theodor-Lieser-Str. 4, D-06210 Halle, Germany*
[2]*Virtual Institute for Macroecology, Theodor-Lieser-Strasse 4, D-06120 Halle, Germany*
[3]*Geldersheimer Straße 64, D-97424 Schweinfurt, Germany*

Abstract. Climate change is one of the most influential drivers of biodiversity. Species-specific differences in the reaction to climate change can become particularly important when interacting species are considered. Current studies have evidenced temporal mismatching of interacting species at single points in space, and recently two investigations showed that species interactions are relevant for their future ranges. However, so far we are not aware that the ranges of interacting species may become substantially spatially mismatched. We developed separate ecological-niche models for a monophagous butterfly (*Boloria titania*) and its larval host plant (*Polygonum bistorta*) based on monthly interpolated climate data, land-cover classes, and soil data at a 10′-grid resolution. We show that all of three chosen global-change scenarios, which cover a broad range of potential developments in demography, socio-economics, and technology during the 21st century from moderate to intermediate to maximum change, will result in a pronounced spatial mismatch between future niche spaces of these species. The butterfly may expand considerably its future range (by 124–258%) if the host plant has unlimited dispersal, but it could lose 52–75% of its current range if the host plant is not able to fill its projected ecological niche space, and 79–88% if the butterfly also is assumed to be highly dispersal limited. These findings strongly suggest that climate change has the potential to disrupt trophic interactions because co-occurring species do not necessarily react in a similar manner to global change, having important consequences at ecological and evolutionary time scales.

Key words: biotic interactions; Boloria titania; *butterflies; climate envelope modeling; ecological-niche modeling; European species-distribution data; global change; host plants;* Polygonum bistorta; *range shift; species interactions; trophic interactions.*

INTRODUCTION

Recent climate change has already affected the distributions of many species (Hill et al. 2001, Parmesan and Yohe 2003, Hickling et al. 2006) but future changes are likely to have even more severe impacts (Sala et al. 2000, Thuiller et al. 2005, Araújo et al. 2006). These impacts are, beside other approaches, often assessed with bioclimatic envelope models that relate the current distribution of species to climatic variables to derive projected future distributions under climate change (e.g., Huntley et al. 2004, Heikkinen et al. 2006). However, the restriction to climatic variables has caused some critique (Davis et al. 1998, Pearson and Dawson 2003) and calls for the consideration of other factors determining species distributions such as dispersal, land cover, and biotic interactions (Guisan and Thuiller 2005, Heikkinen et al. 2006, Ibáñez et al. 2006, Ohlemüller et al. 2006).

Several authors have suggested or demonstrated an increased importance of the speed and extent of climate change in relation to the responses of interacting species. The majority of work has investigated the effects of temporal mismatching at single points in space (Winder and Schindler 2004, Durant et al. 2007, Jonzen et al. 2007, Martin 2007) but we are only aware of two very recent studies analyzing the effect of species interactions on spatial distribution under climate change (Araújo and Luoto 2007, Heikkinen et al. 2007). Nevertheless, there still is a substantial lack of investigation about whether the ranges of interacting species may become spatially mismatched. In this context climate change may have unexpected consequences when the distribution of one species is influenced by the distribution of another species, since even interacting species most likely respond differently to changing conditions.

Here by way of example we analyzed trophic interactions between the monophagous butterfly *Boloria titania* Esper and its larval host plant *Polygonum bistorta* L. (for the assumption of monophagy, see *Discussion*, below). Based on their current European distribution (see Appendices A and B), separate ecological-niche models were developed for the butterfly and its host plant including not only climate parameters and their variations but also land cover and, for the host plant,

soil conditions. We did not simply use the presence of the host plant as an additional predictor for the butterfly, but disentangled the effects of climate change on butterfly distribution from that of host-plant availability. Therefore, we calculated separate models for both species which were then projected to three different global-change scenarios for 2080 resulting in independent potential future distributions, hereafter referred to as "niche space." For the interpretation of the results we made two extreme assumptions about dispersal: (1) there is unlimited dispersal such that the entire projected niche space denotes the actual future distribution; and (2) there is no dispersal, in which case the future distribution results from the overlap between current and future niche space. Potential spatial mismatch of both species' ranges was assessed by the overlap of both future niche spaces.

METHODS

Study area, plant, butterfly, and environmental data

The spatial extent of the study covered EU25 (i.e., the European Union excluding the two 2007 accession states Bulgaria and Romania due to data availability) plus Norway and Switzerland, while the spatial resolution of original data differed between the sources. The host plant *Polygonum bistorta* is distributed across Europe except the northern parts of Scandinavia and central parts of Greece and the Iberian Peninsula and it occurs in humid or wet meadows. Its global distribution extends east as far as Siberia. European distribution data were taken from 1720 grid cells of about 50×50 km^2 from the database of the "Atlas Florae Europaeae" (Lathi and Lampinen 1999). The butterfly *Boloria titania* is a mountain species of Central Europe, the Baltic states and southern Finland occurring in mires and humid flowery meadows, preferably in mountain valleys. Distribution data were taken from about 7000 reference localities, identified by their geographical coordinates, and distributed evenly across the study area. These data also formed the basis of "The Distribution Atlas of European Butterflies" (Kudrna 2002).

Monthly, interpolated climate data were used at a 10'-grid resolution (New et al. 2000, Mitchell et al. 2004). Mean values of the following 20 climate variables for the period 1971–2000 were derived, while regarding absolute values and their variation, which was shown to have particular effects on ecological interactions (Stireman et al. 2005): annual temperature (°C); range in annual temperature (°C); quarterly temperature (e.g., March–May = spring; °C); range in quarterly temperature (°C); diurnal temperature range per year (°C); diurnal temperature range per quarter (°C); annual summed precipitation (mm); range in annual precipitation (mm); quarterly summed precipitation (mm); range in quarterly precipitation (mm); annual water deficiency (annual equilibrium evapotranspiration minus annual precipitation); range in annual water deficiency; annual cloudiness (%); quarterly cloudiness (%); accumulated growing degree days until February, April, June, and August. In total we used 22 626 grid cells.

Percentages of the following five land-cover classes (Mucher et al. 2000) were calculated for the same 10'-grid cells used for the climate variables: forest; grassland; arable land; urban; and others, comprising natural and seminatural areas, water bodies, inland rocks, and ice (Rounsevell et al. 2006).

Percentages of the following eight soil characteristics (European Soil Database 2004) were calculated for the 10' grid cells: parent material; surface texture; available water holding capacity; base saturation; cation exchange capacity; depth to gleyed horizon; depth to rock; topsoil organic carbon content.

Scenarios of global change

Global-change scenarios were based on storylines developed within the European Union (EU)-funded project ALARM (Settele et al. 2005, Spangenberg 2007), which integrated the Intergovernmental Panel on Climate Change (IPCC 2001) Special Report on Emission Scenarios (SRES). The main sources for future climate scenarios were coupled atmosphere–ocean general circulation models (HadCM3; New et al. 2000). The ALARM scenarios (Spangenberg 2007) cover a broad range of potential developments in demography, socio-economics, and technology during the 21st century. The scenario of *moderate change* (SEDG, sustainable-Europe development goal) approximates the IPCC B1 climate-change scenario and assumes that policy will integrate social, environmental and economic aspects in order to enhance the sustainability of societal development. Policy will aim at a competitive economy and a healthy environment, gender equity, and international cooperation. Mean expected temperature increase in Europe until 2080 is 2.4°C. The scenario of *intermediate change* (BAMBU, business as might be usual) approximates the IPCC A2 scenario and assumes free trade, growth, and globalization but policy decisions already made in the EU will be implemented and enforced. Mean expected increase in temperature is 3.1°C. The scenario of *maximum change* (GRAS: growth applied strategy) approximates the IPCC A1FI scenario and assumes that free trade, growth, and globalization will be the main policy objectives. Environmental policies will focus on damage repair and limited prevention based on cost–benefit calculations. Mean expected increase in temperature is 4.1°C.

Based on the storylines, projections of future changes in climate and land use were developed on the 10' grid of Europe. Monthly projected climate data were averaged for the period 2051–2080. Annually projected changes in land use were modeled in a spatially explicit way on the same 10' grid until 2080 (Rounsevell et al. 2006).

Ecological-niche modeling

Climate and soil variables were subject to a principal-components analysis (PCA) and a correspondence

analysis (CA) respectively to maintain full environmental space but avoid collinearity. The first six climate PCs (explained variance = 88.6%) and the first seven soil CA axes (explained variance = 60.0%) were kept together with the five land-cover variables. For future climate conditions, projected axis scores were used.

Ecological-niche models relating environmental variables to presence and absence data were developed using generalized linear models (GLM) with a binomial error distribution and a logit link function. We allowed for additive, curvilinear effects of soil CA axes and land-cover variables, and for multiplicative and curvilinear effects of the climate PCs by incorporating up to third-order polynomials. We used climate, soil, and land-use variables for the plant model and excluded soil variables from the butterfly model. Models were checked for spatial autocorrelation with Moran's I correlograms of model residuals, but none was detected. Initial models were simplified by stepwise regression, while minimizing Akaike's information criterion (AIC; Sakamoto et al. 1986).

The ecological-niche model for the host plant was developed at the 50×50 km^2 grid and then downscaled to the $10' \times 10'$ grid cells (Araújo et al. 2005). While for host-plant modeling the whole area was used, the model for the butterfly was developed only where the host plant is currently present, thus host-plant occurrence does not interfere with the analyses. Models were calibrated on an 80% random sample of the initial data set and model accuracy was evaluated on the remaining 20%. Agreements between observed presences and absences and projected distributions were evaluated by the area under the curve (AUC) of a receiver operating characteristic (ROC) plot, which is independent of thresholds (Fielding and Bell 1997). Thresholds for calculating presence-absence projections were obtained by a maximizing-kappa approach (Manel et al. 2001). The accuracy of downscaling of the host plant was evaluated by investigating whether projected niche space at the $10'$-grid resolution matched the observed distribution at the 50-km grid resolution using AUC.

RESULTS

Both models, for *Polygonum bistorta* and *Boloria titania*, were of high accuracy (AUC [area under the curve] = 0.94 for external evaluation of the plant model at the AFE ["atlas Flora Europaeae"] grid resolution [50 × 50 km], AUC = 0.85 for external evaluation of the plant model for downscaling, and AUC = 0.93 for the butterfly model; see Appendices A and B). Expanding the ecological-niche model of the butterfly to the areas where the host plant is absent indicated a pronounced mismatch between the current potential distribution of the butterfly and that of its host plant. Only a small overlap exists where both species can co-occur (Fig. 1a). All three scenarios of global change for the host plant resulted in a net loss of niche space, a typical northward range expansion, and a general loss and fragmentation

of its current niche space (Fig. 1b, c and Fig. 2; Appendix C). This means that under the assumption of full dispersal the future distribution of *P. bistorta* will be significantly shifted northwards, while under the assumption of no dispersal the future distribution will be considerably reduced (Fig. 1b, c and Fig. 2; Appendix C).

In contrast to *P. bistorta*, global change scenarios for *B. titania*—under full dispersal and unconstrained by the host plant—predicted a net increase of niche space resulting in a higher proportion of new area to be colonized which is most pronounced in the north. However, absolute dispersal limitation of the butterfly would also lead to a significant decrease in its niche space (Fig. 1d, e and Fig. 2; Appendix C).

Overlaying the projected future niche spaces of the butterfly and its host plant under the assumption of unlimited dispersal of both reveals that the observed mismatch between both niche spaces under current conditions will be more pronounced in the future, especially in the areas of current co-occurrence along the Alps and the Baltic states (Fig. 3a, c; compare to Fig. 1a). It was also evident that larger areas in Scandinavia will provide suitable conditions for co-occurrence, leading to a general increase in the niche space of the butterfly and the proportion of niche space that can potentially be realized by co-occurrence with the host plant (Appendix C). However, these new suitable areas are distant and have to be reached by both butterfly and host plant. In case of absolute dispersal limitation of *P. bistorta* (Fig. 3b, d), the mismatch between both niche spaces was extremely high, leading to a substantial decrease for the butterfly in overall niche space and realized niche space (Fig. 2; Appendix C). In the case of no dispersal ability of both species, the spatial mismatch of both niche spaces was most pronounced, resulting in a serious decrease of the future range of the butterfly and its realized niche space (Fig. 2; Appendix C).

DISCUSSION

For the first time, the future distribution of a butterfly is modeled by explicitly realizing the dependence of the butterfly on its host plant in the model design and not by simply including the host plant as an additional predictor (see Araújo and Luoto 2007, Heikkinen et al. 2007). The butterfly *Boloria titania* and its host plant *Polygonum bistorta* exhibit a pronounced mismatch of their current niche spaces. There are large suitable areas mainly in Scandinavia but also in southern Europe where the butterfly potentially could live but is limited by its host plant. On the other hand, there are large parts in temperate Europe where the host plant is present but the butterfly is not. Here, limitation by climate appears as a likely explanation but other biotic interactions, such as predation, competition or parasitism might also contribute.
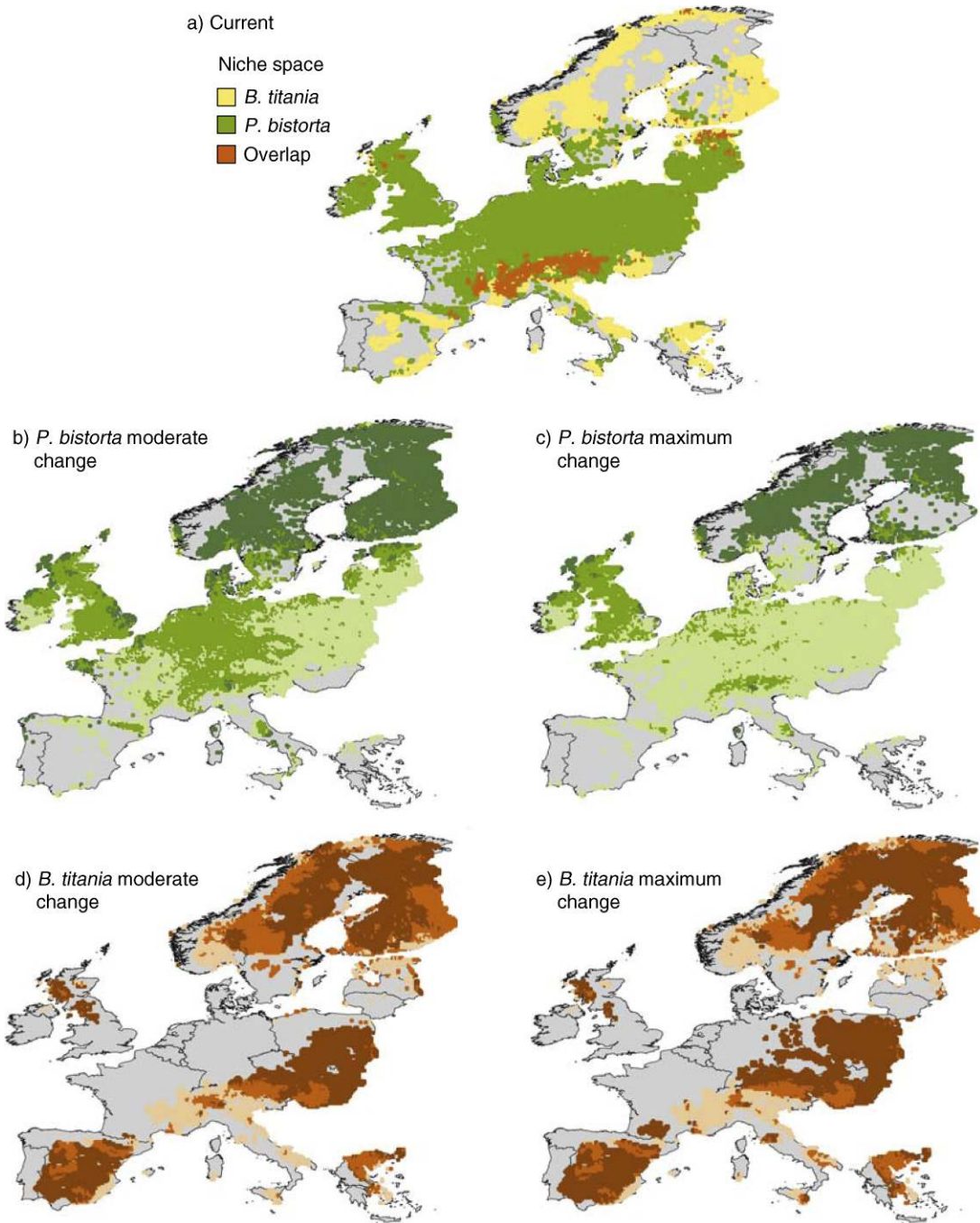
FIG. 1.   Maps of niche spaces of the butterfly *Boloria titania* and its host plant *Polygonum bistorta* under various climate-change scenarios. (a) Current (1971–2000). The "overlap" regions indicate where the two species overlap (realized niche space of *B. titania*). (b, c) Changes in niche space of *Polygonum bistorta* and (d, e) changes in niche space of *Boloria titania* for moderate and maximum global-change scenarios for 2080. Medium green and medium brown indicate remaining niche space in case of no dispersal; dark green and dark brown indicate new niche space; medium green plus dark green and medium brown plus dark brown indicate future niche space in case of unlimited dispersal; light green and light brown indicate lost niche space.

The spatial mismatch of both species was further amplified by climate change. While *B. titania* potentially would benefit from climate change considering climatic niche space (but ignoring the host plant), *P. bistorta* obviously will decrease and therewith *B. titania*. This shows that projections of potential species distributions can be overly optimistic if crucial trophic interactions or habitat requirements are ignored. In the United Kingdom, for instance, most butterfly species are expected to have benefited from recent climate warming (Warren
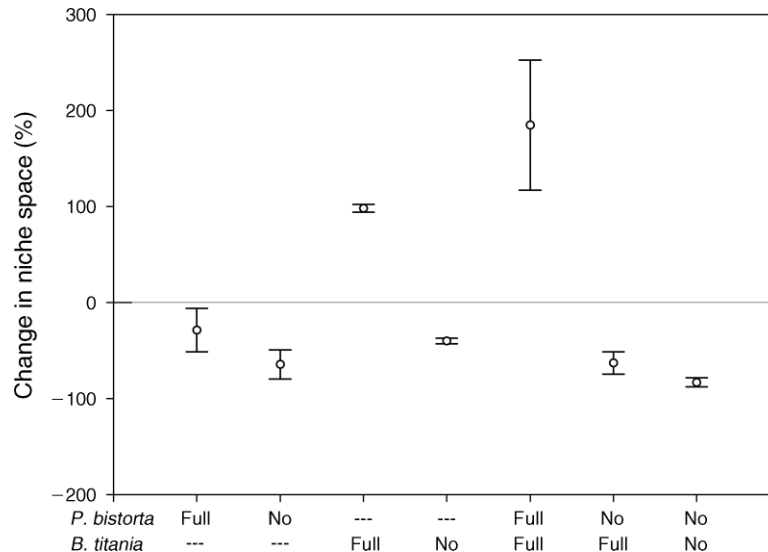
FIG. 2. Changes (means ± SD) in the niche space of *Polygonum bistorta* and *Boloria titania* for three global-change scenarios for 2080 in the case of unlimited dispersal (full) and no dispersal (no). The first two categories on the left depict changes for *P. bistorta*; the other categories depict changes for *B. titania* either unconstrained (third and fourth category) or constrained by *P. bistorta* (fifth to seventh category) for combinations of assumed dispersal abilities. The dashed line indicates no change in the niche space.

et al. 2001) while it was shown that most species actually declined in abundance and range size as a consequence of simultaneously changing landscape characteristics such as habitat availability and landscape structure (Warren et al. 2001, Hill et al. 2002). Since habitat loss and fragmentation at smaller scales and geographical barriers at larger scales impede the ability of species to reach new climatically suitable areas, dispersal characteristics are of great relevance (Hewitt 2000, Clark et al. 2003). In the case of species interactions, the successful colonization of new climatically suitable areas depends on both the dispersal ability of the focal species and that of ecologically linked species, like larval host plants (Hampe 2004).

In our example, assuming either absolute or no dispersal limitation resulted in severely different consequences for *B. titania*. In the case of no dispersal limitation of both species, new potentially suitable areas will occur far in the north of the butterfly's current distribution. This might require long-distance dispersal since it is likely that neither the movement of the plant will be continuous because of heterogeneous patterns of global change nor that the dispersal vectors of the butterfly will be the same. In the case of absolute dispersal limitation of *P. bistorta*, the butterfly is faced with losing suitable area and thus with fragmentation that is even more pronounced when both species are assumed not to disperse (Schtickzelle et al. 2006). To assume dispersal limitation for plants in general is quite sensible under a precautionary approach (Hewitt 2000, Clark et al. 2003). Long-distance dispersal through wind dispersed is quite unlikely for *P. bistorta* because of its relatively high seed mass (~5.5 mg), low number of seeds (~152 per shoot), and their low release height

(0.3–1 m) (LEDA Traitbase, *available online*).[5] However, air in the seedcoat allows dispersal by water, which in principle enables larger dispersal distances and classifies *P. bistorta* as having high potential for long distance dispersal (Wim Ozinga, *personal communication*). But dispersal direction is then determined by the catchment area and does not track continuously the general northwards shift in suitable area. This makes it very unlikely that *P. bistorta* may colonize the majority of new suitable areas in the north of Scandinavia.

B. titania can also be regarded as rather sedentary, according to the classification of many *Boloria* species by Bink (1992). For the similarly classified *B. eunomia*, maximum dispersal distances of 5 km have been reported (Mennechez et al. 2004). Given its univoltine life cycle, this means that within the projected 80 years *B. titania* might move potentially no more than 400 km. Consequently, reality is likely to be better represented by the assumption of no dispersal for both species, while the full-dispersal option is overly optimistic.

Here we have provided evidence that trophic interactions and dispersal limitation matter at continental scales and that they can play a significant role in shaping the dynamic responses of species to climate change. Considering the host plant and two extreme dispersal syndromes turned the very optimistic future projection of the butterflies range distribution into a seriously eroded one. The analyzed trophic interaction is rather basic, but the principle mechanism of changes in spatial matching of interacting species in the course of climate change can be expanded to other inter- and intra-trophic

---

[5] ⟨www.leda-traitbase.org⟩

Unlimited dispersal of *P. bistorta*   No dispersal of *P. bistorta*

a) Moderate change

b) Moderate change
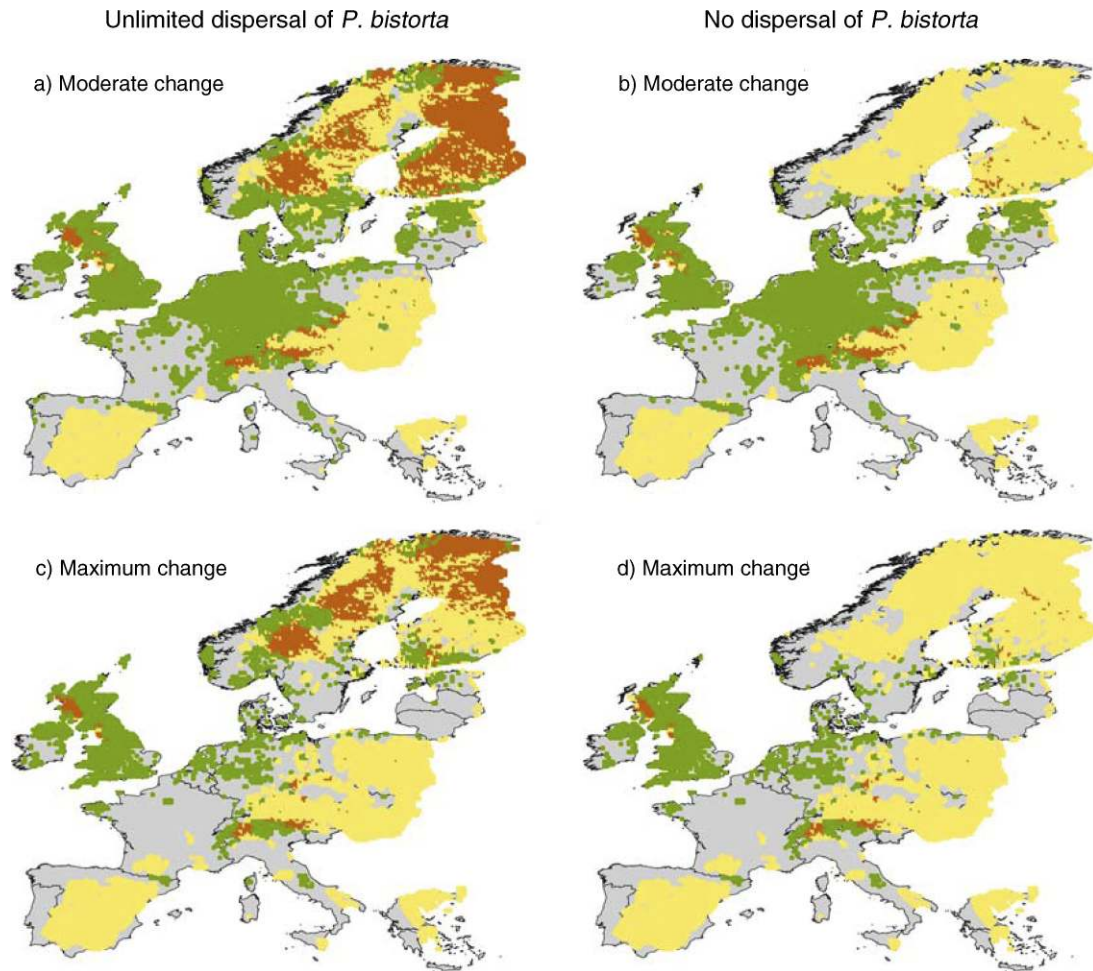
c) Maximum change

d) Maximum change

FIG. 3. Match and mismatch of projected niche spaces of *Polygonum bistorta* and *Boloria titania* for (a, b) moderate and (c, d) maximum global-change scenarios for 2080 under the assumption of unlimited (a, c) and no (b, d) dispersal of *P. bistorta*. Green indicates niche space of *P. bistorta*; yellow indicates niche space of *B. titania*; brown indicates overlap of both (potentially realized niche space of *B. titania*).

interactions. For instance, the distribution of the host plant might not only be limited by climate, which was the assumption in our study, but also by mutualists such as pollinators (e.g., Pigott and Huntley [1981] showed that pollination limitation explained the northern range margin of *Tilia cordata* in the United Kingdom), or by competitors such as taller plants (e.g., Hilbig [1995] showed that taller herbs frequently replace lower congeneric species towards the Eastern range margin of *P. bistorta* in Siberia) or other herbivores. However, *P. bistorta* usually has many pollinators (and the ability of self-pollination), is regarded as quite competitive and stress tolerant and plant stands do not show signs of overexploitation by herbivores (J. Settele, *personal observation*). The same applies to the butterfly. Here competitors (e.g., Kunte 2008), predators (e.g., Langham 2004), parasites (e.g., Lei and Hanski 1997), or diseases might limit its distribution in addition to climate and the host plant. Our study shows that co-

occurring, interacting species do not necessarily react in a similar manner to global climate change. As long as the ranges of interacting species do not perfectly match, they will depend on different sets of climatic and other biotic conditions and thus respond individually. These individual responses might result in more severe consequences or even opposing projections than simple climate-envelope models would suggest. Pronounced negative effects can be a consequence of increased mismatching of beneficial interactions, such as trophic dependencies, as was the case in our study, or better matching of adverse interactions (e.g., limiting competitors or parasitoids). Nevertheless, positive effects could also be a consequence of future better matching of beneficial interactions (e.g., pollination) or more mismatching of adverse interactions (e.g., release of a plant from its herbivore). Consequently, to provide realistic projections of future species distributions other essential biotic interactions have to be considered in addition to

climate (Hampe 2004, Guisan and Thuiller 2005, Heikkinen et al. 2006, 2007, Ibanez et al. 2006, Araújo and Luoto 2007).

Even under a minimum global-warming scenario, changing interactions and the need for dispersal puts strong evolutionary pressures on the affected species. Some evidence for evolutionary responses to climate change, such as changes in flowering time, habitat breath and choice, as well as dispersal behavior, have already been reported (Thomas et al. 2001, Schtickzelle et al. 2006). The spatial mismatching of interacting species and a potential serious decrease in the realized niche puts on high pressure to change essential interactions, e.g., changing the host plant. In several butterfly species that like *B. titania* live on *P. bistorta*, it was observed that in areas where this species cannot be found, they feed on *Viola* species (e.g., *Boloria eunomia* and *Lycaena helle*). This might indicate that such evolutionary adaptations might have taken place in the past. Although for *B. titania* this is anecdotally reported in some textbooks, we could not find any published evidence for real observational data in any of the numerous national butterfly faunas to which we had access. However, even if one should occasionally be able to observe *Viola* as a host plant used by the butterfly's larvae, this will not affect the main result of our study. On the contrary, it rather could be taken as evidence of an ongoing but long-lasting process until such an adaptation will come into effect and, what is more, there is little indication that evolutionary adaptations may keep up with the high speed of global change under more extreme scenarios (compare also Jump and Penuelas [2005]).

LITERATURE CITED

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modeling species distributions under climate change. Global Ecology and Biogeography 16:743–753.

Araújo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712–1728.

Araújo, M. B., W. Thuiller, P. H. Williams, and I. Reginster. 2005. Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. Global Ecology and Biogeography 14:17–30.

Bink, F. A. 1992. Ecologische Atlas van de Dagvlinders van Noordwest-Europa. Schuyt, Haarlem, The Netherlands.

Clark, J. S., M. Lewis, J. S. McLachlan, and J. HilleRis-Lambers. 2003. Estimating population spread: What can we forecast and how well? Ecology 84:1979–1988.

Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391:783–786.

Durant, J. M., D. O. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33:271–283.

European Soil Database. 2004. European Soil Bureau Network and the European Commission, EUR 19945 EN, March 2004. ⟨http://eusoils.jrc.it/ESDB_Archive/ESDB_Data_Distribution/ESDB_data.html⟩

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. Global Ecology and Biogeography 13:469–471.

Heikkinen, R. K., M. Luoto, M. B. Araujo, R. Virkkala, W. Thuiller, and M. T. Sykes. 2006. Methods and uncertainties in bioclimatic envelope modeling under climate change. Progress in Physical Geography 30:751–777.

Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson, and J. H. Korber. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. Global Ecology and Biogeography 16:754–763.

Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. Nature 405:907–913.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12:450–455.

Hilbig, W. 1995. The vegetation of Mongolia. SPB Publishing, Amsterdam, The Netherlands.

Hill, J. K., Y. C. Collingham, C. D. Thomas, D. S. Blakeley, R. Fox, D. Moss, and B. Huntley. 2001. Impacts of landscape structure on butterfly range expansion. Ecology Letters 4:313–321.

Hill, J. K., C. D. Thomas, R. Fox, M. G. Telfer, S. G. Willis, J. Asher, and B. Huntley. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. Proceedings of the Royal Society of London B 269:2163–2171.

Huntley, B., R. E. Green, Y. C. Collingham, J. K. Hill, S. G. Willis, P. J. Bartlein, W. Cramer, W. J. M. Hagemeijer, and C. J. Thomas. 2004. The performance of models relating species geographical distributions to climate is independent of trophic level. Ecology Letters 7:417–426.

Ibáñez, I., J. S. Clark, M. C. Dietze, K. Feeley, M. Hersh, S. LaDeau, A. McBride, N. E. Welch, and M. S. Wolosin. 2006. Predicting biodiversity change: outside the climate envelope, beyond the species–area curve. Ecology 87:1896–1906.

IPCC [Intergovernmental Panel on Climate Change]. 2001. Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Jonzen, N., A. Hedenstrom, and P. Lundberg. 2007. Climate change and the optimal arrival of migratory birds. Proceedings of the Royal Society B 274:269–274.

Jump, A. S., and J. Penuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters 8:1010–1020.

Kudrna, O. 2002. The distribution atlas of European butterflies. Apollo Books, Stenstrup, Denmark.

Kunte, K. 2008. Competition and species diversity: removal of dominant species increases diversity in Costa Rican butterfly communities. Oikos 117:69–76.

Langham, G. M. 2004. Specialized avian predators repeatedly attack novel color morphs of Heliconius butterflies. Evolution 58:2783–2787.

Lathi, T., and R. Lampinen. 1999. From dot maps to bitmaps: Atlas Florae Europaeae goes digital. Acta Botanica Fennica 162:5–9.

Lei, G. C., and I. Hanski. 1997. Metapopulation structure of Cotesia melitaearum, a specialist parasitoid of the butterfly Melitaea cinxia. Oikos 78:91–100.

Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38:921–931.

Martin, T. E. 2007. Climate correlates of 20 years of trophic changes in a high-elevation riparian system. Ecology 88:367–380.

Mennechez, G., S. Petit, N. Schtickzelle, and M. Baguette. 2004. Modelling mortality and dispersal: consequences of parameter generalisation on metapopulation dynamics. Oikos 106:243–252.

Mitchell, T. D., T. R. Carter, P. D. Jones, M. Hulme, and M. New. 2004. A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100). Tyndall Centre for Climate Change Research, University of East Anglia, Norwich, UK.

Mucher, C. A., K. T. Steinnocher, F. P. Kressler, and C. Heunks. 2000. Land cover characterization and change detection for environmental monitoring of pan-Europe. International Journal of Remote Sensing 21:1159–1181.

New, M., M. Hulme, and P. Jones. 2000. Representing twentieth-century space-time climate variability. Part II: Development of 1901-96 monthly grids of terrestrial surface climate. Journal of Climate 13:2217–2238.

Ohlemüller, R., E. S. Gritti, M. T. Sykes, and C. D. Thomas. 2006. Quantifying components of risk for European woody species under climate change. Global Change Biology 12:1788–1799.

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

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Pigott, C. D., and J. P. Huntley. 1981. Factors controlling the distribution of Tilia cordata at the northern limits of its geographical range. III. Nature and causes of seed sterility. New Phytologist 87:817–839.

Rounsevell, M. D. A., et al. 2006. A coherent set of future land use change scenarios for Europe. Agriculture, Ecosystems & Environment 114:57–68.

Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike information criterion statistics. D. Reidel Publishing Company, Dordrecht, The Netherlands.

Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Schtickzelle, N., G. Mennechez, and M. Baguette. 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. Ecology 87:1057–1065.

Settele, J., et al. 2005. ALARM: Assessing LArge scale environmental Risks for biodiversity with tested Methods. GAIA—Ecological Perspectives in Science, Humanities, and Economics 14:69–72.

Spangenberg, J. H. 2007. Integrated scenarios for assessing biodiversity risks. Sustainable Development 15:343–356.

Stireman, J. O., et al. 2005. Climatic unpredictability and parasitism of caterpillars: Implications of global warming. Proceedings of the National Academy of Sciences (USA) 102: 17384–17387.

Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. Nature 411:577–581.

Thuiller, W., S. Lavorel, M. B. Araujo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences (USA) 102:8245–8250.

Warren, M. S., et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65–69.

Winder, M., and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85:2100–2106.

APPENDIX A

A map showing the current (1971–2000) distribution of Polygonum bistorta (Ecological Archives: E089-198-A1).

APPENDIX B

A map showing the current (1971–2000) distribution of Boloria titania (Ecological Archives: E089-198-A2).

APPENDIX C

A table showing projected changes in niche space of Polygonum bistorta and Boloria titania for moderate, intermediate, and maximum global-change scenarios for 2080 (Ecological Archives: E089-198-A3).