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The importance of biotic interactions for modelling species distributions under climate change

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ABSTRACT

Aim There is a debate as to whether biotic interactions exert a dominant role in governing species distributions at macroecological scales. The prevailing idea is that climate is the key limiting factor; thus models that use present-day climate–species range relationships are expected to provide reasonable means to quantify the impacts of climate change on species distributions. However, there is little empirical evidence that biotic interactions would not constrain species distributions at macroecological scales. We examine this idea, for the first time, and provide tests for two null hypotheses: ($H_0 1$) – biotic interactions do not exert a significant role in explaining current distributions of a particular species of butterfly (clouded Apollo, *Parnassius mnemosyne*) in Europe; and ($H_0 2$) – biotic interactions do not exert a significant role in predictions of altered species' ranges under climate change.

Location Europe.

Methods Generalized additive modelling (GAM) was used to investigate relationships between species and climate; species and host plants; and species and climate + host plants. Because models are sensitive to the variable selection strategies utilised, four alternative approaches were used: AIC (Akaike's Information Criterion), BIC (Bayesian Information Criterion), BRUTO (Adaptive Backfitting), and CROSS (Cross Selection).

Results In spite of the variation in the variables selected with different methods, both hypotheses ($H_0 1$ and $H_0 2$) were falsified, providing support for the proposition that biotic interactions significantly affect both the explanatory and predictive power of bioclimatic envelope models at macro scales.

Main conclusions Our results contradict the widely held view that the effects of biotic interactions on individual species distributions are not discernible at macroecological scales. Results are contingent on the species, type of interaction and methods considered, but they call for more stringent evidence in support of the idea that purely climate-based modelling would be sufficient to quantify the impacts of climate change on species distributions.

Keywords

Bioclimatic envelope models, climate change, cross-validation, clouded Apollo butterfly, Europe, macroecology, *Parnassius mnemosyne*, sensitivity analysis, uncertainty.

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INTRODUCTION

Attempts to forecast climate-change impacts on biodiversity have often relied on the bioclimate 'envelope' modelling approach, whereby present-day distributions of species are combined with environmental variables to enable projected

distributions of species under future climate scenarios (e.g. Berry *et al.*, 2002; Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Araújo *et al.*, 2006). The validity of this approach has been questioned on the grounds that important biotic interactions – in particular interspecific competition – are not taken into account within models (e.g. Davis *et al.*, 1998; Leathwick, 2002). In response to

this criticism it has been proposed that biotic interactions might play a relatively minor role in governing species distributions at regional to continental scales (Pearson & Dawson, 2003), where climate is expected to exert a dominant role. We investigate this idea and ask whether the inclusion of simple biotic interactions in bioclimate 'envelope' models (here the presence and absence of four larval host plants of the genus *Corydalis*) would significantly alter predictions of climate-change impacts on one particular species of butterfly (clouded Apollo, *Parnassius mnemosyne*; Linnaeus, 1758) distributed across Europe. In contrast to previous studies that investigated the role of interspecific competition in the predictive performance of models at local to regional scales (Leathwick & Austin, 2001; Anderson *et al.*, 2002; Leathwick, 2002), our analyses focus on the rather more neglected phenomena of parasitism at a continental scale.

The idea that biotic interactions could affect the predictions of bioclimate 'envelope' models was explored by Davis *et al.* (1998). The authors used a simple microcosm experiment including three fruit fly species (*Drosophila* spp.) and a parasitoid wasp (*Leptopiliana boulandi*) to show the impact of interspecific competition on the distribution of species under simulated climate change. Using a particular cline of 15 °C it was demonstrated that competition markedly altered the distributions of all three fruit fly species in comparison with those found in single-species clines. Under simulated warming, unexpected effects on the distribution and abundance of fruit fly species were produced, including the reversal of the species' relative abundance at some temperatures. The authors concluded that biotic interactions should be included in predictions of species' responses to climate change, without which predictions from bioclimate envelope models could be misleading. The conclusions of this study were challenged by Hodkinson (1999), who provided evidence of cases where species' distributions were directly affected by climate.

One potential criticism to the conclusions made by Davis *et al.* (1998) is that the scaling up of results of a microcosm experiment to macroecological scale may not be appropriate. Indeed, it is widely contended that processes operating at a local scale (such as interspecific competition or parasitism) do not exert a similarly dominant role at macroecological scales (e.g. Huston, 1999; Whittaker *et al.*, 2001). Pearson & Dawson (2003) proposed a hierarchical framework for modelling whereby climate would be expected to exert a dominant role in governing species' distributions across regional and continental scales (e.g. > 200 km), whereas biotic interactions would be expected to play a major role at local scales (e.g. < 1 km) (see also Pearson *et al.*, 2004). The framework proposed by Pearson and Dawson is drawn from a tradition followed by a number of ecologists, including Whittaker (1975) who showed that the distribution of the main terrestrial biomes of the world could be explained by the distribution of mean temperature and precipitation values alone (see also Holdridge, 1947). The idea that climate would govern the distribution of biota at macro scales was also supported by recent studies showing that species distributions models, including climate variables, would have a greater degree of explanatory and predictive power than models including land-cover variables at

continental (Europe, Thuiller *et al.*, 2004) and regional scales (Britain, Pearson *et al.*, 2004; Great Lakes Basin including parts of Canada and USA, Venier *et al.*, 2004; Finland, Luoto *et al.*, 2006).

Even though climate is known to affect the distributions of species, there is limited evidence in support of the companion idea that biotic interactions would not play a major role constraining current and future species distributions at macroecological scales. Here, we examine this idea and provide a test of the null hypotheses that: ($H_0 1$) – biotic interactions do not exert a significant role in explaining current distributions of a particular species of butterfly in Europe; and ($H_0 2$) – biotic interactions do not exert a significant role in predicting species distribution shifts under climate change scenarios. Testing hypotheses about the mechanisms underlying species' responses to climate change is problematic, not least because events being tested have not yet occurred (Araújo *et al.*, 2005b). Furthermore, when hypotheses concern processes operating at macroecological scales, the problem is entangled by the difficulty in designing fully controlled experiments (Brown, 1995). An alternative is to use what we term here 'surrogate hypotheses'. Surrogate hypotheses are expected to correlate with the hypotheses under investigation, but they are assessed from an examination of patterns in the data rather than by the processes causing them. The falsification of surrogate hypotheses provides an indirect and thus less powerful protocol for hypothesis testing than standard manipulative experiments. However this is a familiar – and often necessary – procedure in macroecology, where a starting null hypothesis is often that the observed pattern is a simple consequence of the null expectation (Gotelli & McGill, 2006). The difficulty in discerning cause and effect may be partly surmounted by offering repeated evidence of patterns using a variety of surrogate hypotheses applied to different taxa and regions (e.g. Blackburn & Gaston, 1998; Gaston & Blackburn, 1999). Even when such evidence is provided it may be difficult to separate correlation from causation. Here we formulate three surrogate hypotheses and discuss the context in which they can be seen as providing support or dismissal for the two null hypotheses under investigation.

DATA AND METHODS

Species data

The European distribution of the clouded Apollo butterfly was digitized from the atlas *Butterflies of Europe* (Kudrna, 1985) and resampled to the 50 × 50 km *Atlas Flora Europaeae* (AFE) grid system (Jalas & Suominen, 1972–1996) to allow matching with other data (Fig. 1). Individual AFE cells were classified as 'clouded Apollo present' if more than 50% of the European butterflies atlas cells covered per AFE cell had the species recorded as present. Host plants associated with the larval state of the clouded Apollo butterfly were identified from the literature (see Luoto *et al.*, 2001, and references therein) and included four species of the genus *Corydalis*: *C. solida*, *C. intermedia*, *C. cava* and *C. pumila*. European distributions of the four *Corydalis* species were obtained from a digitised version of AFE (Lahti & Lampinen, 1999).

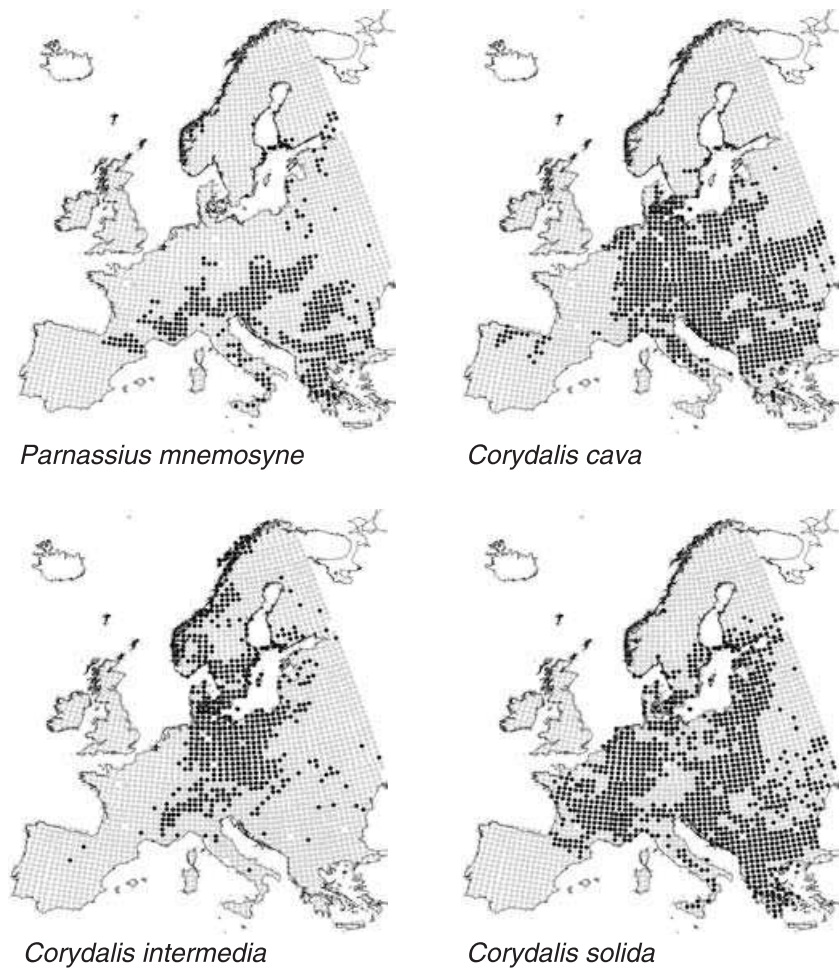


Figure 1 European distribution of the clouded Apollo butterfly (*Parnassius mnemosyne*) and the three species of the genus *Corydalid* that are known to act as larval host plants.

Climate data

A set of aggregated climate parameters was derived from an updated version of the monthly climate data of New *et al.* (2000). The updated data provide monthly values for the years 1901–2000 on a $10' \times 10'$ spatial resolution (Mitchell *et al.*, 2004). Average monthly temperature and precipitation in grid cells covering the mapped area of Europe were used to calculate mean values of six different climate parameters for the period of 1961–1991 (referred to as baseline data). Variables included: mean annual temperature within time slices (TANN; °C); mean temperature of the coldest month (MTC; °C); mean annual summed precipitation (PANN; mm); mean sum of precipitation between July and September (PSUM; mm); mean sum precipitation between December and February (PWIN; mm); and growing season (GDD), defined as the mean annual growing degree days (> 5 °C). Choice of variables was made to reflect two primary qualities of the climate – i.e., energy and water – that, on the basis of prior knowledge, have known roles in imposing constraints upon plant and butterfly species distributions as a result of widely shared physiological limitations (e.g., Prentice *et al.*, 1992; Hill *et al.*, 1999; Parmesan *et al.*, 1999). We used one climate change scenario produced by the HadCM3 GCM (Hadley Centre for Climate Prediction and Research general circulation model)

averaged for the period of 2036–2065 (referred to as 2050 scenario, Schröter *et al.*, 2005) using the A1FI (fossil intensive) emission scenario (Nakicenovic & Swart, 2000). We used only one scenario because our prime interest was to assess the sensitivity of models to the inclusion of biotic interactions rather than to the GCM or emission scenarios used.

Modelling

Generalised Additive Models (GAMs; Hastie & Tibshirani, 1990) were fitted to assess three types of relationships: species–climate (hereafter termed GAM climate); species–host plants (hereafter termed GAM host plant); and species–climate + host plants (hereafter termed GAM climate + host plant). Predictor variables were smoothed with four degrees of freedom. Because models are sensitive to the variable selection procedures utilized (for discussion see Araújo & Guisan, 2006, and Heikkinen *et al.*, 2006), four alternative approaches were used: AIC (Akaike's Information Criterion; Akaike, 1974), BIC (Bayesian Information Criterion; Schwartz, 1979), CROSS (Cross Selection; Stone, 1977), and BRUTO (Adaptive Backfitting; Hastie & Tibshirani, 1990). These four approaches were first applied and compared in the context of species distribution modelling by Maggini *et al.* (2006).

Table 1 Modelling design for: (a) testing the null hypothesis ($H_0 1$) – that biotic interactions do not exert a significant role in explaining current distributions of the clouded Apollo butterfly (*Parnassius mnemosyne*) in Europe; and (b) testing the null hypothesis ($H_0 2$) – that biotic interactions do not exert a significant role in predicting species distribution shifts under climate change scenarios.

(a)

1. Split clouded Apollo distribution data randomly into calibration (70%) and validation (30%) sets and repeat the procedure 10 times to obtain different data for calibration and evaluation of models.
2. Run AIC, CROSS, BIC and BRUTO generalized additive models (GAMs) with climate predictors alone (GAM climate) for each one of the 10 randomly derived calibrations sets (40 model runs).
3. Run AIC, CROSS, BIC and BRUTO GAMs with *Corydalis* host plant predictors (GAM host plant) alone for each one of the 10 randomly derived calibrations sets (40 model runs).
4. Run AIC, CROSS, BIC and BRUTO GAMs with climate and host plant predictors (GAM climate + host plant) for each one of the 10 randomly derived calibrations sets (40 model runs).
5. Transform modelled species probabilities of occurrence from the 120 models (obtained in steps 2, 3 and 4) into predictions of presence and absence of clouded Apollo using a cut-off defined by prevalence.
6. Evaluate GAM models by measuring agreement between observed and modelled distributions of clouded Apollo using Kappa and AUC procedures.

(b)

7. Model *Corydalis* species distributions with climate predictors (AIC, BIC, BRUTO and CROSS GAMs) and project their potential distributions in 2050 with the A1FI HadCM3 GCM model (models).
8. Transform modelled probabilities of occurrence from models using a cut-off defined by prevalence (as in step 5).
9. Generate two scenarios of future potential distributions of *Corydalis*: (i) with unlimited dispersal (species are able to disperse to areas with suitable environments); and (ii) with no dispersal (species are unable to disperse to areas with suitable environments, thus only being able to lose potential range).
10. Project distributions of the clouded Apollo butterfly in 2050 with the A1FI HadCM3 GCM model. For GAM climate + host plant and GAM host plant use modelled *Corydalis* distributions from steps 7 and 8.

Models were calibrated using a 70% random sample of the clouded Apollo butterfly distribution and evaluated against the remaining 30% of the data (for details on the design of the modelling experiment see Table 1). This procedure of cross validation was repeated ten times (yielding a 10-fold cross validation) to assess the sensitivity of projections to variations in the data used for calibration of the models (i.e., the initial conditions), thus providing a measure of model stability. Modelled species probabilities of occurrence were transformed into presence and absence records using a cut-off defined by the prevalence (the proportion of species occurrences among all grid cells) of clouded Apollo butterflies in the studied area. This approach for identification of cut offs is attractive for its simplicity and because it has been shown to be at least as effective as the more complex sensitivity-specificity sum maximization, sensitivity-specificity equality and ROC plot based approaches (for discussion see Liu *et al.*, 2005). Evaluation of models consisted of measurements of agreement between observed and modelled distributions obtained by calculating the Cohen's Kappa statistic index of similarity (Kappa) and the area under the curve (AUC) of the receiver operating characteristic (ROC) (Fielding & Bell, 1997).

The European distribution of the clouded Apollo butterfly was projected into the future using the A1FI HadCM3 GCM climate scenario for 2050, and assuming unlimited dispersal (i.e., the species is able to track climate changes and disperse to areas with suitable environments); this assumption was considered to be reasonable given the evidence that butterfly species are already responding to observed climate changes by swift tracking of their climate envelope (e.g. Wilson *et al.*, 2005; Hickling *et al.*, 2006). Again three models were used: GAM climate; GAM host plant; and GAM climate + host plant. To fit the two latter models we

projected distributions of *Corydalis* species for 2050 and included projected distributions as covariates in the models. Because we were unable to make robust statements about the dispersal ability of the *Corydalis* species we considered two extreme scenarios of dispersal: unlimited dispersal (as for the clouded Apollo butterfly); and no dispersal (species unable to track climate changes thus contract whenever portions of their range become climatically unsuitable). The 'truth' regarding the dispersal of these three species is likely to lie somewhere in the middle. Future potential distributions of *Corydalis* species were modelled with GAM climate, using the same procedure adopted for modelling the clouded Apollo butterfly (for more details see Table 1).

All models were fitted with the GRASP v. 3.1 package (Lehmann *et al.*, 2003) for S-PLUS (Insightful Corp., Seattle, USA). Kappa and AUC calculations were carried out using SPSS v. 10 for Windows (Norusis, 1999).

Hypothesis testing

To test the first null hypothesis ($H_0 1$) that biotic interactions do not exert a significant role in explaining current distributions of the clouded Apollo butterfly in Europe, we formulated two surrogate hypotheses: ($SH_0 1.1$) – stepwise AIC, BIC, BRUTO and CROSS GAM models fitted with the possibility of selecting covariates representing both climate and host plants (i.e., occurrence of *Corydalis* species) will not select host plants; and ($SH_0 1.2$) – estimators of model performance (i.e., explained deviance on calibration (D^2), Kappa, and AUC values estimated on the evaluation data) will not vary significantly ($P > 0.05$) between GAM climate and GAM host plant models and between

GAM climate and GAM climate + host plant models. If the result of the first test is that host plants are selected by stepwise models, then we falsify SH_0 1.1 and support the alternative hypothesis that variables accounting for biotic interactions might matter. If the inclusion of host plants as predictor variables leads to improvements in model performance, then additional support for the alternative hypothesis that biotic interactions matter is obtained.

Ideally, the second hypothesis (H_0 2), that biotic interactions do not exert a significant role in predictions of species distributions shifts under climate change scenarios, should be tested with independent evaluation data (Araújo *et al.*, 2005a). Such data were unavailable to us and they are unlikely to become available at macroecological scales. Consequently, we performed a sensitivity analysis to assess how model outputs varied when different sets of predictor variables (with and without biotic-interaction terms) are used. More specifically, we examined the surrogate hypothesis (SH_0 2.1) that projections of species range shifts under climate change with GAM climate, GAM host plant, and GAM climate + host plant are not significantly different from each other. The underlying assumption is that if the inclusion of host plants as covariates in the models has no discernible effect in projections of altered species distributions under climate change, then its use is unnecessary. Of course, falsifying this hypothesis, i.e., demonstrating that a variable has an effect in a model output, does not prove that the effect is useful. However, falsification of SH_0 2.1 can lead to an interpretation that inclusion of biotic interactions within models is useful for making projections of future species distributions if SH_0 1.2 is also falsified (host plant variables improve estimates of model performance with non-independent data).

Agreement of model projections was measured using the Kappa statistic (e.g. Monserud & Leemans, 1992). Differences in model outputs produced with climate, host plant, and climate + host plant covariates (SH_0 1.2, and SH_0 2.1) were tested using Wilcoxon signed-rank tests for related samples. Statistical tests were carried out using SPSS v. 12 for Windows.

RESULTS

GAM climate models consistently selected the same four temperature and precipitation variables, whilst summer precipitation and growing degree days were less likely to be selected (Table 2). When the occurrence of *Corydalis* host plants was considered alongside climate variables (GAM climate + host plant), the models selected three climate variables consistently (now including summer precipitation) and the host plant *Corydalis solida* (Table 2). When models were fitted using the occurrence of host plants alone (GAM host plant), *Corydalis solida* and *C. cava* were selected consistently by all models, whereas *C. intermedia* was excluded by all BIC models and *C. pumila* was selected only twice with the CROSS method. Whilst confirming the importance of energy and water related variables, these results also highlight the importance of including the presence of the host plant *C. solida* to explain the distribution of clouded Apollo butterfly at the macro scale in Europe, thus falsifying the surrogate null hypothesis

Table 2 Variables selected in 'GAM climate', 'GAM host plant' and 'GAM climate + host plant models'. Model selection is based on forward-backward stepwise AIC (Akaike's Information Criterion), BIC (Bayesian Information Criterion), BRUTO (Adaptive Backfitting), and CROSS (Cross Selection). A 10-fold cross validation procedure was adopted so that 10 model runs were performed for each selection and the number of times each variable was selected was counted.

	AIC	BIC	BRUTO	CROSS	Mean
GAM climate					
GDD	0	0	5	10	3.75
TANN	10	10	10	10	10
MTC	10	10	10	10	10
PANN	10	10	10	10	10
PSUM	10	0	6	10	6.5
PWIN	10	10	10	10	10
GAM host plant					
<i>Corydalis solida</i>	10	10	10	10	10
<i>C. intermedia</i>	10	0	10	10	7.5
<i>C. cava</i>	10	10	10	10	10
<i>C. pumila</i>	0	0	0	2	0.5
GAM climate + host plant					
GDD	0	0	5	10	3.75
TANN	10	2	6	10	7
MTC	9	0	10	10	7.25
PANN	10	10	10	10	10
PSUM	10	10	10	10	10
PWIN	10	10	10	10	10
<i>C. solida</i>	10	10	10	10	10
<i>C. intermedia</i>	0	0	0	3	0.75
<i>C. cava</i>	0	0	1	3	1
<i>C. pumila</i>	2	0	3	5	2.5

GDD, mean annual growing degree days (> 5 °C); TANN, mean annual temperature within time slices (°C); MTC, mean temperature of the coldest month (°C); PANN, mean annual summed precipitation (mm); PSUM, mean sum of precipitation between July and September (mm); PWIN, mean sum precipitation between December and February (mm).

(SH_0 1.1) that models fitted with the possibility of selecting covariates representing both climate and host plants would not select host plants.

All measures of model performance, i.e., explained deviance (D^2), Kappa and ROC values were lowest with GAM host plant followed by GAM climate then GAM climate + host plant, irrespective of the variable selection procedure used (Table 3). Model performance was significantly different ($P < 0.01$ for D^2 and $P < 0.05$ for Kappa and AUC) between GAM host plant and GAM climate, and between GAM climate and GAM climate + host plant (Table 3). In other words, both the 'explanatory' (in calibration) and 'predictive' power of models (in non-independent validation, *sensu* Araújo *et al.*, 2005a) were greater with climate than with host plant models, but models were significantly improved (except when using BIC) when host plants were considered alongside climate variables. These results provide a falsification of the surrogate null hypotheses (SH_0 1.2) that

Model	Variable selection	D ² (cal.)	Kappa (eval.)	AUC (eval.)
Climate	AIC	0.291 ± 0.015	0.417 ± 0.038	0.847 ± 0.018
	BIC	0.282 ± 0.016	0.419 ± 0.042	0.844 ± 0.019
	BRUTO	0.268 ± 0.015	0.401 ± 0.044	0.839 ± 0.020
	CROSS	0.292 ± 0.015	0.417 ± 0.039	0.847 ± 0.017
Host plant	AIC	0.182 ± 0.011**	0.323 ± 0.027*	0.788 ± 0.016*
	BIC	0.179 ± 0.011**	0.324 ± 0.026*	0.783 ± 0.017*
	BRUTO	0.182 ± 0.011**	0.323 ± 0.027*	0.788 ± 0.016*
	CROSS	0.182 ± 0.011**	0.323 ± 0.027*	0.788 ± 0.016*
Climate + host plant	AIC	0.363 ± 0.014**	0.438 ± 0.033*	0.880 ± 0.013*
	BIC	0.341 ± 0.014**	0.421 ± 0.028	0.874 ± 0.015*
	BRUTO	0.341 ± 0.014**	0.427 ± 0.033*	0.873 ± 0.015*
	CROSS	0.366 ± 0.014**	0.443 ± 0.035**	0.880 ± 0.013*

* $P < 0.05$; ** $P < 0.01$ (based on Wilcoxon signed-rank tests for related samples assessing differences between: climate versus host plant models; and climate versus climate + host plant models).

Model	AIC	BIC	BRUTO	CROSS
Climate				
AIC	0.91; 0.02**	0.83; 0.04**	0.85; 0.03**	0.91; 0.03**
BIC		0.93; 0.02**	0.90; 0.03**	0.83; 0.04**
BRUTO			0.91; 0.03**	0.84; 0.04**
CROSS				0.91; 0.02**
Host plant				
AIC	1.00; 0.00	0.99; 0.01**	0.99; 0.02**	0.99; 0.01**
BIC		1.00; 0.00	0.99; 0.01**	1.00; 0.01**
BRUTO			1.00; 0.00	0.99; 0.01**
CROSS				1.00; 0.00
Climate + host plant				
AIC	0.94; 0.03**	0.90; 0.02**	0.90; 0.02**	0.93; 0.02**
BIC		0.97; 0.01**	0.91; 0.01**	0.89; 0.02**
BRUTO			0.93; 0.02**	0.90; 0.02**
CROSS				0.92; 0.02**

** $P < 0.001$ (based on Wilcoxon signed-rank tests for related samples assessing (in bold) 'intra' model-selection agreement (e.g. Climate AIC) and 'inter' model-selection agreement (e.g. Climate AIC vs. Climate BIC)).

estimators of model performance would not vary significantly between GAM climate and GAM climate + host plant.

Spatial projections of the future distribution of the clouded Apollo butterfly in Europe differed visibly across the GAM climate, GAM host plant, and GAM climate + host plant (Fig. 2), suggesting that the incorporation of a biotic interaction term in the models has an effect in the projections of future species' potential distributions.

Projections were more similar (Wilcoxon signed-rank test, $P < 0.001$) when models were calibrated with a combination of climate and host plant variables (mean 'within' model-selection-technique agreement Kappa = 0.94; mean 'between' model-selection-technique agreement Kappa = 0.91) than when models were calibrated with climate predictors alone (mean 'within' model-selection-technique agreement Kappa = 0.92; mean

Table 3 Mean model performance measures applied to climate and climate-interaction models. D² = explained deviance of the model calibration data (cal.). Kappa and area under curve (AUC) values are based on evaluation data set (eval.). The threshold for Kappa is based on prevalence of data used for model calibration. AIC, Akaike's Information Criterion; BIC, Bayesian Information Criterion; BRUTO, Adaptive Backfitting; CROSS, Cross Selection.

Table 4 Kappa values (as a measure of agreement) and standard deviation of these values among modelled future distributions of the clouded Apollo butterfly (*Parnassius mnemosyne*) (assuming unlimited dispersal of the host plants). AIC, Akaike's Information Criterion; BIC, Bayesian Information Criterion; BRUTO, Adaptive Backfitting; CROSS, Cross Selection.

'between' model-selection-technique agreement Kappa = 0.86) (see Table 4 for all results). Pure host plant models produced almost identical projections (mean 'within' model-selection-technique agreement Kappa = 1.00; mean 'between' model-selection-technique agreement Kappa = 0.99), because the presence of *Corydalis solida* dominated the structure of all models. In other words, models using host plants as predictor variables projected the presence of clouded Apollo when *C. solida* was present and the absence of clouded Apollo when *C. solida* was absent; this was true even when other *Corydalis* species were present. More importantly, the degree of coincidence between model projections (GAM climate versus GAM climate + host plant, mean Kappa = 0.70, SD = 0.03; and GAM climate versus GAM host plant, mean = 0.40, SD = 0.02) was also significantly lower (Wilcoxon signed-rank test, $P < 0.001$) than the degree of

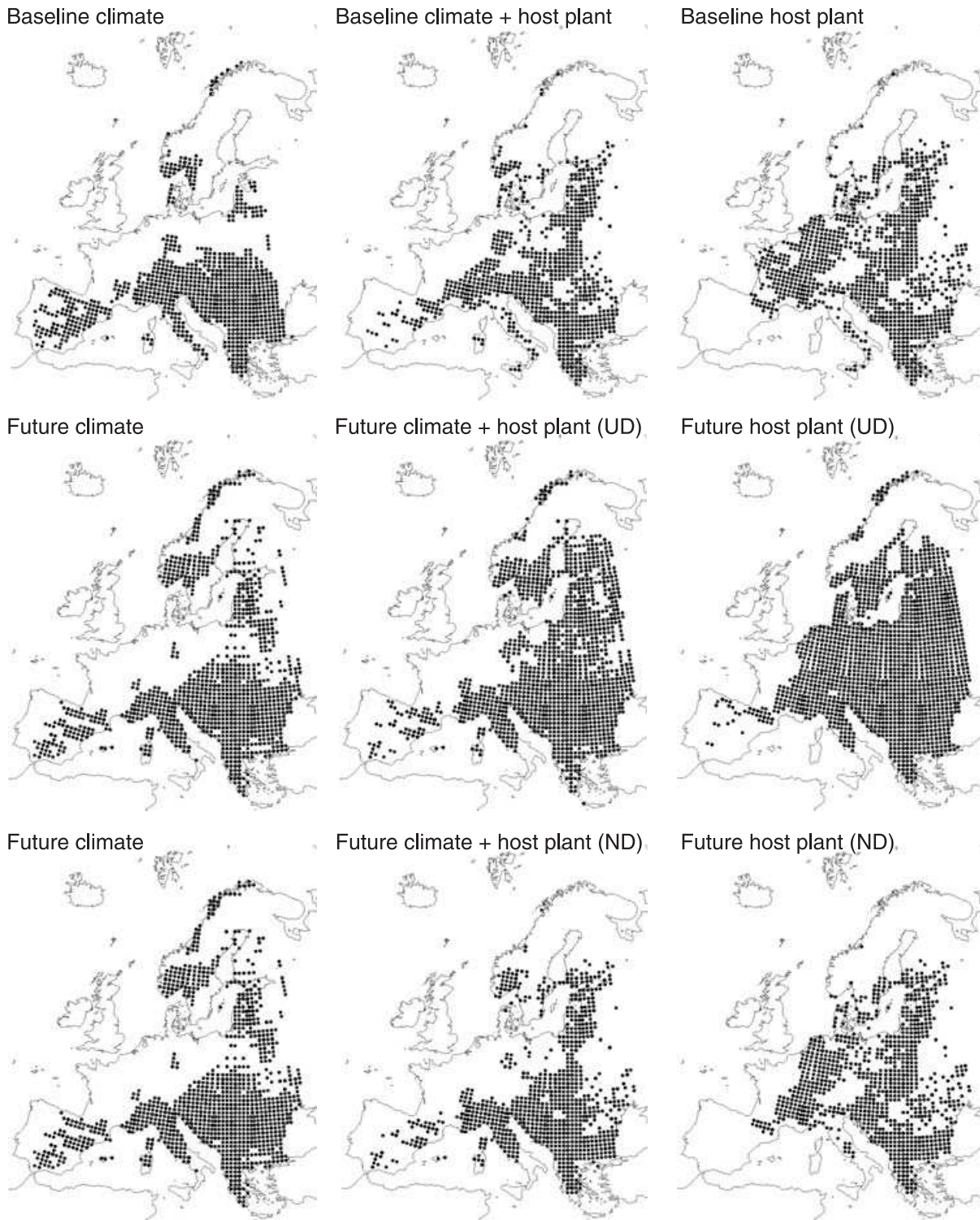


Figure 2 European modelled distribution of the clouded Apollo butterfly (*Parnassius mnemosyne*) for baseline and future (2050) conditions assuming unlimited dispersal (UD) and no dispersal (ND) among larval host plants, *Corydalis* spp. Results for the three model outputs (one Akaike's Information Criterion (AIC) generalized additive model (GAM) out of ten simulations of initial conditions) are presented: (first column) climate model; (second column) climate + host plant model; and (third column) host plant model.

coincidence within overall model projections (mean $Kappa = 0.92$; $SD = 0.03$). These latter results provide a falsification of the surrogate null hypothesis ($SH_0 2.1$) that differences in projections of species range shifts under climate change with GAM climate, GAM host plant, and GAM climate + host plant are not significantly different from each other.

DISCUSSION

The three surrogate null hypotheses formulated to investigate the idea that biotic interactions would not exert a dominant role at macroecological scales were falsified. These results invite the interpretation that more stringent evidence is required to support the conjecture that present-day species–climate relationships would suffice to allow realistic estimates of species' responses to climate change at macroecological scales. Previous studies investigating the potential implications of biotic interactions on empirical modelling of species distributions have offered evidence that the explanatory power of models at a local to regional scale could be affected by biotic interactions, such as interspecific competition (Leathwick & Austin, 2001; Anderson *et al.*, 2002; Leathwick, 2002). Here, we provide evidence that biotic interactions might also matter at macroecological scales; that they affect models of altered species' distributions under climate change scenarios; and that, apart from negative interactions such as interspecific competition, positive and neutral interactions are also likely to play a role in shaping the dynamic responses of species to changes in climate. This latter observation coincides with evidence from empirical (e.g. Callaway *et al.*, 2002) and simulation (e.g. Travis *et al.*, 2005) experiments that positive interactions can be predominant, especially in conditions of abiotic stress that are typical of periods of accelerated climate change. Our results also show that if climate and biotic interactions are considered in isolation, there is a higher likelihood that the former would yield models with higher explanatory and predictive values.

Nevertheless, an appropriate interpretation of our results requires an assessment of the assumptions and limitations of our analyses. At least three issues deserve discussion. Firstly, it is important to acknowledge that we modelled only one species and its identity was not chosen at random: the species was selected because there was a suggestion that at least three host plant species would be important to explain its distribution at local and landscape levels (e.g. Luoto *et al.*, 2001; Heikkinen *et al.*, 2005). It is thus open to debate whether the results obtained with the clouded Apollo butterfly in Europe are representative of larger samples of species, although a previous study using a different species at a smaller spatial scale (both grain and extent) coincides with our conclusion that the inclusion of positive biotic interactions into bioclimatic 'envelope' models may increase their performance (Gutiérrez *et al.*, 2005). The importance of positive interactions for modelling species' responses to climate change is likely to be related to the degree of species' specialisation within assemblages of a given region; the more specialized species assemblages are, the more dependent they should be on the fate of other species. Huntley (1997)

argued that most species are generalists rather than specialists, but this pattern is likely to be spatially uneven (Julliard *et al.*, 2006). Indeed, a distinction has often been made between the relative importance of abiotic and biotic interactions, with the latter typically being regarded as being more important at lower latitudes (e.g. Dobzhansky, 1950; MacArthur, 1972).

Secondly, we used an indirect hypothesis-testing protocol based on surrogate hypotheses. This is a familiar approach in macroecology but one that is less powerful than using fully controlled experiments. For example, there is a risk that including species distributions as predictor variables in a model of another species might not truly reflect a biotic interaction but simply the absence of important environmental predictors in the model (e.g. Guisan & Thuiller, 2005). In the case of this study we had *a priori* knowledge on the biology of the clouded Apollo butterfly, so there was a robust mechanistic basis for choosing biotic interaction predictors among many alternatives; this may not always be possible.

Thirdly, the results are sensitive to the data and statistical techniques used. Although the multiple variable selection and cross-validation procedures adopted in this study are a first step towards exploring sensitivities of model outcomes to variations in input data and to variable selection functions, there are other sources of variability that were not explored here (e.g. Johnson & Omland, 2004). For example, some variable selection procedures differ between modelling techniques. Hence, different techniques might select different variables, thus compromising the conclusions of any study that uses one modelling technique alone. Furthermore, we did not explore the full breadth of variable selection techniques available. There are a number of relatively unexplored approaches such as multi-model inference, boosting and model averaging, shrinkage methods, or hierarchical partitioning coupled with randomization procedures that may allow for more robust variable selection estimates (for discussion, see Araújo & New, 2007).

Despite the potential shortcomings and uncertainties of our analysis, this is the first study that explicitly addresses the consequences of incorporating simple biotic interaction terms for modelling species responses to climate change at macroecological scales. Our results have two important implications. From a fundamental standpoint, they support the widely held conjecture that climate is the main determinant of species' distributions at macroecological scales, although the companion idea that biotic interactions play a minor role in governing distributions of species at macroecological scales is not fully supported. From an applied perspective, the results also stimulate questions about the appropriateness of making forecasts of species range shifts without taking into account relevant biotic interactions (see also Davis *et al.*, 1998). Naturally, the critical issue is not whether biotic interactions matter at macroecological scales, but how much? This is a difficult question to answer because we lack independent validation data for testing the impact of biotic interactions on model outputs under climate change conditions (Araújo *et al.*, 2005a), and even if we were offered such a validation set there would be epistemological difficulties in confirming whether agreement between observed and predicted events

Table 5 Projected mean percentage species loss (extinction) and colonization of the clouded Apollo butterfly (*Parnassius mnemosyne*) based on climate, climate + host plant, and host plant models under a scenario of severe climate change (A1FI HadCM3). Projections are made considering both assumptions of unlimited dispersal and no dispersal among the host plants.

	Climate	Climate + host plant	Host plant
Unlimited dispersal			
Extinction	19.1	18.1	10.7
Colonization	36.2	69.4	69.9
No dispersal			
Extinction	19.1	29.4	25.0
Colonization	36.2	29.1	13.6

would provide unequivocal validation of models (Oreskes, 1998). Nevertheless, our results suggest that lack of consideration of host plant distributions within models – or arguably any other biotic relevant interaction – has important consequences for assessing climate change impacts on species distributions. For example, estimates of potential range shifts of clouded Apollo butterflies varied from 19.1% loss of suitable European grid cells (climate model) to 29.5% (climate + host plant model assuming no dispersal of the host plant), whereas gains of suitable cells varied between 13.6% (host plant model assuming no dispersal) and 69.9% (host plant model assuming unlimited dispersal of host plant; climate model projecting 36.2% cell gains) (Table 5).

Clearly it is difficult to obtain sufficient knowledge and data to parameterise macro-scale species distribution models that include complex biotic interactions. There is the further complication that biotic interactions measured for a given time t_1 in a given locality might not hold true for a time t_2 subject to climate change (e.g. Klanderud & Totland, 2005). To disentangle this Gordian knot we need to move towards greater integration of multiple-scale ecological studies, whereby relationships at site to landscape levels are measured and used to inform macro-scale species' distribution models; these measured relationships should, in turn, be tested against coarse-resolution presence-absence data in a similar vein to that used in this study (but see also Leathwick & Austin, 2001; Anderson *et al.*, 2002; Leathwick, 2002). If such communication between researchers working at different spatial scales is not achieved we might need to wait many years until more definite answers to the problem addressed here are provided.

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