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Improving species distribution models using biotic interactions: a case study of parasites, pollinators and plants

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Abstract

Biotic interactions have been considered as an important feature in species distribution modeling, but little is known about the effect of including different types of interactions or performing different strategies of integrating biotic interactions in species distribution modelling. This study compares different methods for including interspecific interactions in species distribution models for bees, their cleptoparasites, and the plants they pollinate. Host-parasite interactions among bumble bees (genus *Bombus*: generalist pollinators and brood parasites) and specialist plant-pollinator interactions between *Centris* bees and *Krameria* flowers were used as case studies. We used 7 different modelling algorithms available in the BIOMOD R package. Adding biotic information to present day predictions of potential occurrence significantly improved the cross-validated area under the receiver operating characteristic curve (AUC), a measure often applied to estimate model accuracy. Different species and types of interaction showed different AUC results in line with data quality, level of biological linkage and interdependence of each interaction. Furthermore, the species that presented the best improvement of AUC was projected under future climate scenarios. The results showed marked differences when using abiotic data only, and when including biotic interactions of various types. The results show that choosing the correct biotic information, based on biological and ecological knowledge, is critical to improve the accuracy of species distribution models, and also to forecast distribution change.

Keywords

Species distribution modelling, species interactions, host-parasite, plant-pollinator, climate change, BIOMOD, *Bombus, Centris, Krameria*

Introduction

Species distribution modelling has been used as a computational tool with multiple objectives, including predicting the impacts of global change, especially global warming (Franklin 2009). This technique combines occurrence data with environmental variables based on a correlative approach to build a representation of a species' ecological requirements (Anderson et al. 2003). Several algorithms have been applied to create such models, and their computational results can show areas that are similar to those where the species is known to occur and thus may represent its potential areas of occurrence (Stockwell and Peters 1999, Phillips et al.

2006). Future scenarios can be projected assuming that current climatic requirements of a species remain unchanged under climate change (Thuiller et al 2005).

Recently, the inclusion of biotic information as input in species distribution models (SDM) has been advocated as a way of representing effects of interspecific interactions (e.g. competition, predation, parasitism, mutualism) on species distributions. For example, plant–insect interactions (Jiménez-Valverde et al. 2008) and specialized plant-pollinator interactions (Godsoe et al. 2009, Giannini et al. 2010, Warren et al. 2010) have been modelled. In most cases incorporating biotic interactions significantly improved the models of the focal species' present day distribution and altered the projections of its future distribution (Araujo and Luoto 2007, Meier et al. 2010, Van der Putten et al. 2010).

Once the biotic information has been selected it can be incorporated in the modelling exercise in different ways. First, the actual points of occurrence of the interacting species might be added directly as a predictor variable for the focal species. This might make sense when the biotic component has an obligate relationship with the focal species. Alternatively, the estimated occurrence or habitat suitability of the interacting species (i.e. its SDM prediction) can be used as input layer in the focal species' models. To our knowledge, a comparative analysis considering both options has not been performed.

The potential value of biotic information to species distribution models should depend on the relationship between the focal species and the biotic component. The occurrence of an obligate parasite, for example, can be taken as good evidence for the presence of its host. While the presence of a single food plant species of a generalist forager merely points to the potential occurrence of that forager species. It is even possible that information on a non-interacting species can improve the distribution model if both species happen to be associated with similar environmental features (e.g. soil, climate, microhabitat). However, previous studies have only compared abiotic SDMs to biotic models that incorporate known interacting species (Heikkinen et al. 2007, Pellissier et al. 2010). As such, it is not clear whether the inclusion of interacting species improves the model because it actually represents interspecific interactions or whether the improvement simply arises through the inclusion of an additional spatially structured predictor.

In this paper, we tested to what extent the modeling methods, trophic position, and level of ecological dependence actually change the SDM of the focal species. We chose two different groups of interacting organisms: one group of host-parasite pairs and one group of specialized plant-pollinator species. The host-parasite group was comprised of species of bumblebees and their conspecific brood parasites (both *Bombus* spp.) that are common throughout Europe and Asia and tend to have a broad floral diet (Benton 2006). The specialized plant-pollinator group was comprised of species of *Krameria* plants (Krameriaceae) and *Centris* bee pollinators - two genera with a Neotropical distribution. *Krameria* plants are pollinated only by *Centris* bees that collect floral oil to raise their offspring (Vogel 1974, Simpson 1989).

The main objectives of this work were 1) to compare the fit of species distribution models with and without biotic data included in different ways; 2) to compare the effect of including biotic data on interacting species pertaining to different trophic positions or ecological dependence; 3) to analyze to what extent projections under climate change depend on modelling methods and the way biotic interactions are included.

Material and Methods

The selected species of *Bombus*, representing host-parasite pairings, were: 1) *B. terrestris* (host) and *B. vestalis* (parasite), and 2) *B. lucorum*, *B. cryptarum* and *B. magnus* (all hosts) and

B. bohemicus (parasite of all three hosts). Analyzes were focused on Great Britain for which good distribution records were available.

The selected species of bees and plants representing pollinator-plant interactions were: 1) *Krameria erecta* (plant)*; Centris atripes* and *C. rhodopus* (pollinating bees) all occurring in western areas of Mexico and USA, and 2) *K. tomentosa* (plant) and *C. fuscata* and *C. tarsata* (pollinating bees) occurring in northeastern and central areas of Brazil.

To compensate for variation in data sampling density between different areas, we created a subsample of our original dataset by overlaying a 10x10 km grid, sampling only one species presence point from each cell (Godsoe et al. 2009). This procedure was performed with ArcGIS 9.3 (ESRI Inc.). The details about data sources used to perform the models can be found as Supplementary Material.

The BIOMOD package (Thuiller 2003) for R 2.11.1 (The R Foundation for Statistical Computing) was applied to model present day and future species distributions. We created pseudo-absence points for each Neotropical species using the BIOMOD "circles" strategy. With this strategy, a circle is drawn individually around each presence point with a radius of 5° and pseudo-absence points selected from this region. The total number of pseudo-absences per species was set so that the number of occurrences and pseudo-absences summed to 10000 (Van der Wal et al. 2009, Lobo and Tognelli 2011). For Britain, where biological recording of bumblebees is good, we selected occurrences reported since the year 1990 and considered the cells with no reported occurrence as true absence points. The original databases were randomly split in calibration (80%) and evaluation subsets (20%) (Fielding and Bell 1997).

Using BIOMOD, we applied 7 model classes: artificial neural networks (ANN) (Ripley 1996), classification tree analysis (CTA) (Breiman et al. 1984), generalised linear models (GLM) (McCullagh and Nelder 1989), generalised boosted models (GBM) (Ridgeway 1999), flexible discriminant analysis (FDA) (Hastie et al. 1994), multivariate adaptive regression splines (MARS) (Friedman 1991) and random forest (RF) (Breiman 2001). We used the cross-validated area under the receiver operating characteristic curve (AUC) to evaluate the models. Swets (1988) suggested that the results of AUC could be interpreted as follows: excellent, when above 0.90; good, between 0.90-0.80; fair, between 0.80-0.70; poor, between 0.70-0.60; and fail, between 0.60-0.50.

We used 19 bioclimatic variables with a grid resolution of 5 arc-minutes to model the species' geographical distributions. These represent gradients in average temperature and precipitation, over diurnal, seasonal and annual timescales (Hijmans et al. 2005). The same variables were used for predicted future climate conditions in 2050, assuming a moderate climatic change scenario (Special Report on Emission Scenarios B2) (Ramirez and Jarvis 2008) and the HADCM3 model (Gordon et al. 2000). In modelling the present day species distributions, we also used land use information for the year 2000 (Global Land Cover 2000 database) that was converted to 10km resolution. Because many of the environmental variables were highly correlated we applied principal component analysis (PCA) using R 2.11.1 (The R Foundation for Statistical Computing) (Powney et al. 2010). We identified six independent axes of variables representing 80% of the total environmental variation in Britain, 97% in North America and 92% in South America.

We added the information about biotic interaction as a supplementary layer to the six PCA variables following different strategies. First, we performed modelling with only the abiotic variables to obtain the probability of occurrence of each species. Second, we created new models including the biotic information in two different ways: (A) We included the actual presence-absence of the biotic component as a supplementary explanatory variable (predictor) to modelling the focal species; (B) We included the occurrence probability of interacting species from abiotic SDMs as a supplementary predictor. Where the modeled

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species had more than one interacting species (e.g. *B. bohemicus* with its hosts and *Krameria* with its pollinators), we fitted individual models for each interacting species, as well as models in which all interacting species were included individually, and models based on the richness of the interacting species. Where models were based on occurrence probabilities, a richness index was derived as the sum of probabilities for the interacting species.

As well as modeling effects of interacting species, we repeated the modeling exercise specifying non-relevant interactions in the SDMs, i.e. we included interactions between species that do not strongly interact via specialist host-parasite or plant-pollinator relationships. In this way, we aim to test whether the AUC variation was due to increased model complexity or statistical artifacts of spatially structured predictors. It was not possible to apply this procedure to *Krameria* species because the different interacting species groups occupied distinct geographic regions. Thus, we considered non-relevant interactions between parasitic *Bombus* species and hosts they did not use, and interactions between regionally co-occurring *Centris* bees. Differences in the resulting AUC evaluations of the abiotic and different biotic models were tested using paired *t* tests.

We also analyzed the effect of including biotic data on model projections with future climate conditions. Future land use scenarios were not available to us, and so for this exercise we developed present day models based on just the climate and interspecific interactions. For brevity, we only forecasted the distribution of the species for which biotic interactions had the largest effect on the SDMs for present day conditions (*B. bohemicus*). To obtain future projections, we applied the ensemble forecasting strategy to these models (Araújo and New 2007, Thuiller et al. 2009). With BIOMOD ensemble forecasting, the final model is a consensual result of all models used (in our case, the same seven models described before), weighted on the basis of their predictive accuracy on the test data. Using this function, one could choose also different kinds of measures of accuracy and we have chosen AUC to calculate the weights.


Results

Including relevant interactions in the SDMs for *Bombus* species nearly always significantly increased their fit, as measured by the AUC score (Fig. 1a). Furthermore, in every case the effect on the parasite species was stronger than that on the host. For the parasite with multiple hosts (*B. bohemicus*), there was little difference between models that used all three hosts individually, used host richness or only used the most widespread host (*B. lucorum*), but inclusion of the rarer hosts resulted only in slight model improvement. Results from models including non-relevant interactions between species not engaged in host-parasite relationships were mixed (Fig. 1b). Unexpected significant improvements in AUC were obtained for three of the eight models, while significant decreases in AUC were obtained in two cases. Indeed, including a non-host of *B. vestalis* (*B. lucorum*) gave a similar model improvement seen when the correct host was included.

On the other hand, the inclusion of biotic interactions in models for the Neotropical plant and pollinator species resulted in almost no significant AUC variation (Figure 1c-d). Significant improvement was observed only in one case when including relevant interactions (*K. erecta* including *C. atripes*) and when including non-relevant species (*C. fuscata* with *C. tarsata*).
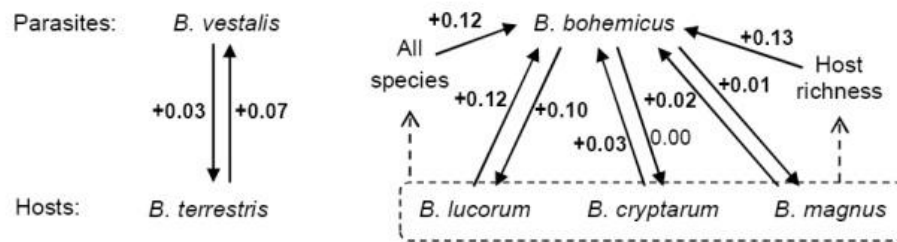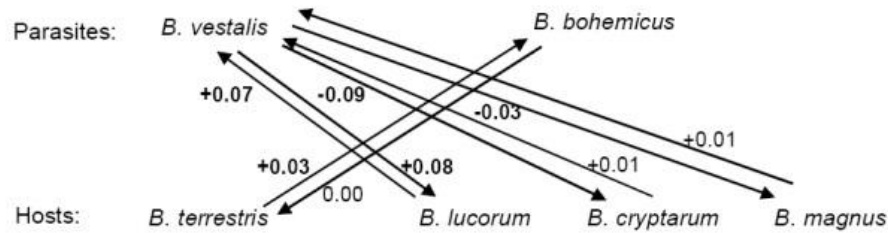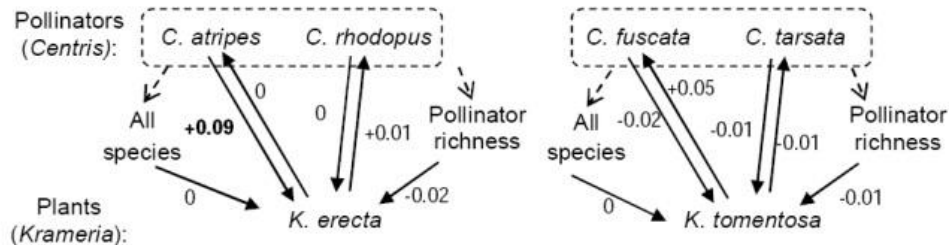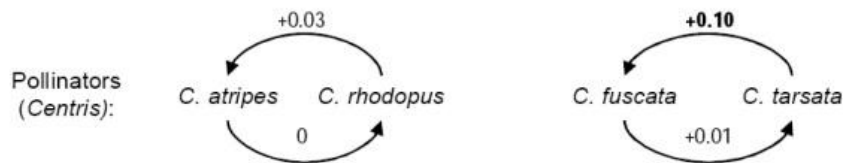
Figure 1. Summary of the effects of including (A) expected actual and (B) non-expected hypothetical interactions between host and brood parasite *Bombus* bumblebees in species distribution models for Great Britain. Interactions were modelled by including the presence/absence of the other species as a predictor alongside six abiotic gradients. Arrows point towards the modelled species and are labelled with the change in average cross-validated AUC caused by including the biotic interaction over the seven modelling algorithms. Bold labels show statistically significant differences (*P* < 0.05 in paired t-tests). For *B. bohemicus*, which has three host species, host richness and all species were also included as a predictor. (C and D) Specialist plant-pollinator interactions between *Centris* bees and *Krameria* flowers. Here species interactions are included by using the abiotic-only distribution model scores for the interactor species as a predictor variable. For both *Krameria* species, richness and both pollinators were included as a predictor. Because of geographical separation between the two species groups, it was not possible to test for unexpected interactions other than between co-occurring pollinators.

The best models for each of the species showed high fits (cross-validated AUC range 0.74-0.98). The resulted average of each variable importance to each model (7 models quoted) was converted to percentage and compared (Figure 2A and B). This measure is a function of the correlation scores between the original prediction and the prediction made with a permuted variable (Thuiller et al. 2009a). The results to host-parasite species showed that the biotic component was the most important variable in the SDMs of focal species and thus more important than any single climate or environmental variable (i.e. PCA axis) (Figure 2A). Considering plant-pollinator (Figure 2B), the average variable importance of interacting species was also higher than PC1 scores, but the results showed higher variation considering PC1 and interacting species.
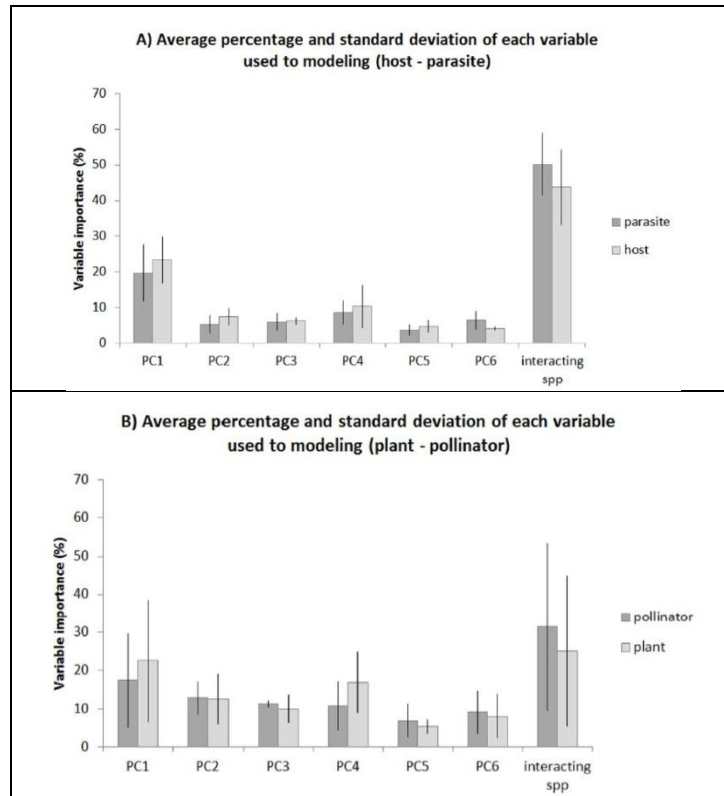

Figure 2. Variable importance of each principal component (abiotic features) and interacting(s) species (biotic feature). Top: Host-parasite; Bottom: Plant-Pollinator.

Model projections of distributions in 2050 with moderate climate change were sensitive to the inclusion of interspecific interactions. For *B. bohemicus* (the species with the highest improvement in AUC for biotic models), abiotic models and biotic models with appropriate and inappropriate interactions all give similar representations of the present-day distribution (Figure 3a-d). However, projections under climate change differ markedly. The abiotic model and the biotic model based on a non-existent interaction both predict that *B. bohemicus* will retreat into its present-day range core in Scotland (northwest Britain) (Figure 3e and h). By contrast, both biotic models suggest the species will maintain or expand its Scottish distribution and also expand into Wales (southwest Britain) (Figure 3f-g).
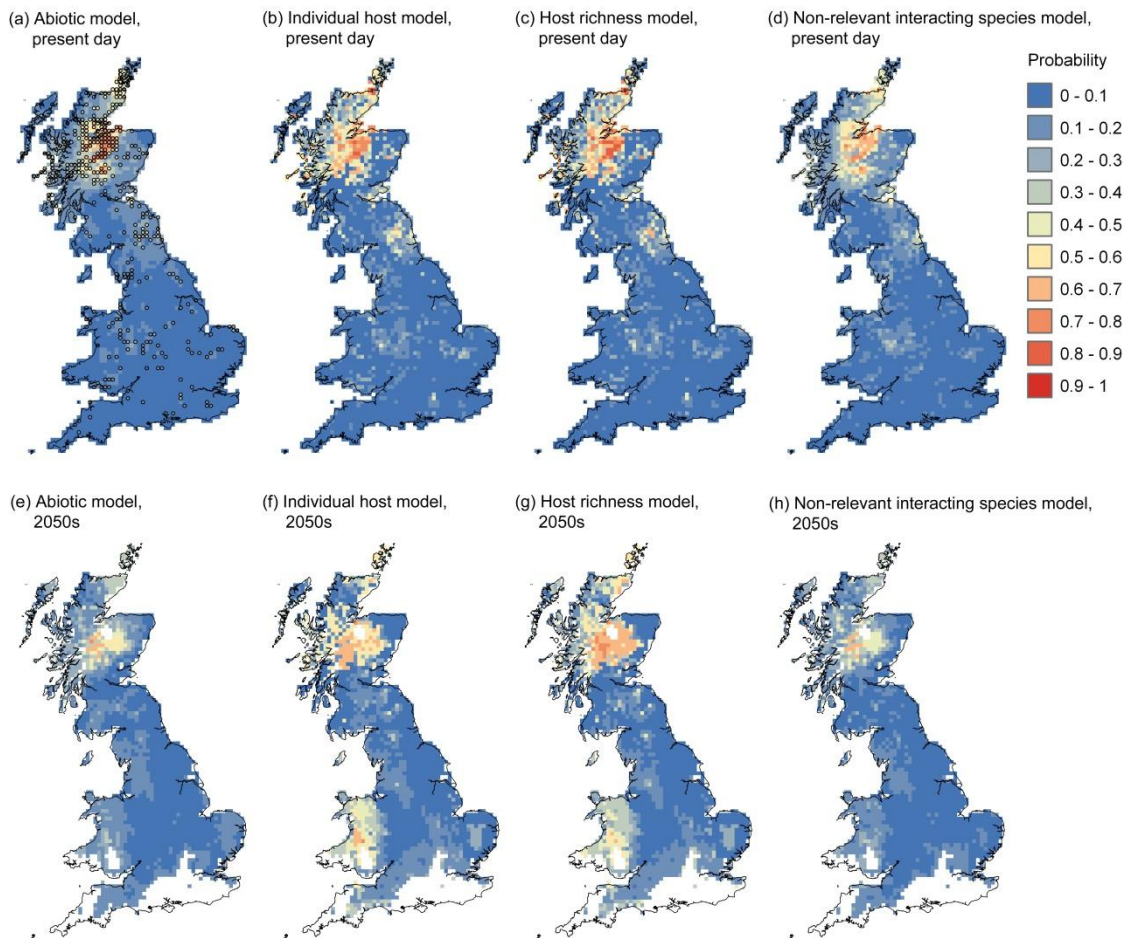
Figure 3. Projections of *Bombus bohemicus* occurrence areas. Top: present climatic conditions using a) abiotic information only; b) *B. lucorum*; c) richness of its three host species (*B. lucorum, B. magnus* and *B. cryptarum*); d) non-relevant interacting species (*B. terrestris*). Bottom: 2050 climatic conditions using e) abiotic information only; f) *B. lucorum*; g) richness of its three host species (*B. lucorum, B. magnus* and *B. cryptarum*); h) non-relevant interacting species (*B. terrestris*). White areas in the future projection maps show the regions where one or more of the climatic PCA gradients are outside the present day range, and on which projections may be unreliable.

Discussion

We found that including interspecific interactions of known relevance to the focal species, resulted in large increases in model fit compared to abiotic models for host-parasite species pairs, but had little effect for plant-pollinator species. This could be due to better data quality in Great Britain than in the neotropics. Alternatively, the interactions among *Bombus* species might be more specialized than those between *Krameria* and *Centris. Krameria* plants depend more on the *Centris* bees (their only pollinator) than the bees depend on *Krameria* oil rewards, since these bees can obtain their resource from other oil plant producers, such as Malpighiaceae species (Simpson 1989). *Centris* is also a widespread genus and other congeneric species could potentially pollinate the *Krameria* species analyzed here. Thus, our results suggest that stronger and more specialized biotic interactions are likely to be more important than weak and generalized interactions in determining regional-scale distribution patterns.

Our results revealed an improvement in *Bombus'* model accuracy when including known strong interspecific interactions in species distribution models. However, in some cases information on non-relevant species also improved the model. Indeed, when modeling *B. vestalis* the non-host *B. lucorum* gave the same increase in model fit as its true host *B.*

terrestris. This might be due to unknown indirect interactions between the species, but is most likely caused by similarity in their relationship with climate and environmental conditions. Therefore, our results show that previous knowledge about species interactions is necessary to establish which biotic information should be added to distribution models and also to correctly interpret the results (i.e. what is the underlying ecological or biological mechanism).

For *Bombus*, the higher trophic level (parasite) always benefited more from including interactions than lower level (host). This may reflect a mainly bottom-up control of host-parasite communities, as suggested by Vazquez et al. (2007) who analyzed trophic networks. One would certainly expect hosts to be able to exist in areas unsuitable for their parasites, but not the other way around. Recent reviews also emphasize that higher trophic levels are often disproportionately affected by drivers such as climate change, competition from invasive species, and habitat modification (Tylianakis et al. 2008, Gilman et al 2010).

We also demonstrated that SDM projected distributions under climate change are sensitive to the inclusion of biotic interactions, as illustrated by our *B. bohemicus* projection to 2050. Analyzing trophic networks, Chen et al. (2008) showed that host species occupying prominent network positions have many interacting partners and the associated parasite species are buffered against fluctuations in host availability; if an interacting partner goes extinct, the parasite can use alternative hosts to continue its life-cycle and survive. Our analysis featured a parasite with few hosts (three species) and so one would expect changes in the distribution of these hosts to be very important in its response to ongoing global change. In any case, our results suggest that a failure to include biotic interactions, or their mis-specification, causes great uncertainty in SDM-based climate change projections. This brings into question earlier studies that predict biodiversity impacts of global change by modeling single-species range shifts without regard for interspecific interactions (Thuiller et al. 2005, Rebelo et al. 2010).

Other works have already reviewed the importance of considering biotic interactions when analyzing impacts of climatic change (Brooker et al. 2007, Hegland et al. 2009, Van der Putten et al. 2010). The analyses addressed here highlight the importance of considering different methods to include this information, and also the importance of reliable knowledge about focal species biology. Our analyzes also support the utility of the "community modules" approach of Gilman et al (2010) whereby entire food webs are simplified into tractable sub-webs of strongly interacting species. In our study, these modules represent defined host-parasite and plant-pollinator linkages. Ferrier and Guisan (2006) also emphasized that predicting the effects of climate change is dependent upon identifying those interactions between species that are most vulnerable to changing climate and are key determinants of the structure and function of a community.

In this study we considered specialized, presumably quite strong interactions. However, weak interactions dominate communities, and it is not clear whether a species' response to climate change would be more influenced by a small number of strong interactions *versus* a large number of weak ones. Such weak interactions might be better represented by multivariate distribution model approaches that represent interspecific associations or shared responses to environmental gradients and predict the distributions of multiple species (Baselga and Araújo 2009; Elith and Leathwick 2007). According to Tylianakis et al. (2008) the presence of weak interactions has long been known to promote web stability and can promote the stability of metacommunities at landscape scales. On the other hand, specialized pollinators, especially ones with small diet breadths, are vulnerable to disruption in the plant community (Memmott et al 2007). As pointed out by Gilman et al. (2010), the key question is not the resulting effects of climate change on individual species, but the stability of the system as a whole.

Conclusions

In conclusion, we found that the distributions of species that have strong and specialized interactions with a focal species are useful predictors in species distribution models. However, including non-relevant interactions can also yield a model improvement, showing that positive correlations between species distribution patterns are not necessarily indicative of interspecific interactions. Furthermore, we also showed how projections of climate change impacts on species distributions are very sensitive to the specification of biotic interactions. Thus, we suggest that a better understanding of species interactions, and how species assemblages face global changes as an integrated system, is needed to understand their resilience to these impacts.

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