

UC Santa Cruz

UC Santa Cruz Electronic Theses and Dissertations

Title

Refining species distribution models for coevolving plant and insects using species interactions and phylogeography

Permalink

<https://escholarship.org/uc/item/0wb7d573>

Author

Schwind, Christopher John

Publication Date

2016

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

**Refining species distribution models for coevolving plant and insects using
species interactions and phylogeography**

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF ARTS

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Christopher Schwind

December 2016

The Thesis of Christopher Schwind
is approved:

Professor John N. Thompson

Professor Kristy Kroeker

Professor Erika Zavaleta

Tyrus Miller
Vice Provost and Dean of Graduate Studies

Table of Contents

Abstract.....	iv
Acknowledgements.....	v
Introduction.....	1
Methods.....	5
Results.....	12
Discussion.....	21
Supplemental Information.....	28
References.....	30

List of Figures

Figure 1.....	13
Figure 2.....	14
Figure 3.....	16
Figure 4.....	18
Figure 5.....	20
Figure 6.....	21
Supplemental Figure 1.....	29

Abstract

Refining species distribution models for coevolving plants and insects using species interactions and phylogeography

Christopher Schwind

Species Distribution Models (SDMs) are the primary tool used to predict the future niche spaces for species. These models, however, do not usually incorporate species interactions that may restrict available niche space. Analysis of the widely studied coevolving network of *Greya* moths and *Lithophragma* plants shows that incorporating species interactions into SDMs can produce results that differ greatly from models without species interaction effects. This effect is highly variable, however, even among very closely related species. Moreover, choosing different phylogenetic levels to run SDMs can alter the predictions greatly, but this effect is also highly variable. The differences among projections that incorporate species interactions and phylogenetics, and those that include neither effect, may result from the relative ranges of these species and populations, and their relationships to each other. We also show here how these models predict changes in the particular combinations of plant and insect species that interact in each region, which could, in turn, lead to yet more cascading effects on the future of the geographic distributions of these coevolving lineages of interacting species.

Acknowledgements

I'd like to thank John Thompson for his support and mentorship over our long history of working together. Most of what I've learned about how to be a scientist, I've learned from John. I'd also like to thank Erika Zavaleta and Kristy Kroeker for their guidance and direction on this project. I've also learned a great deal from former Thompson Lab members, Magne Friberg, Paulo Guimarães, Jason Hoeksema, and Catherine Fernandez. Thank-you all for the really useful conversations we've had over the years. Thank-you to my parents, who always encouraged me to think critically and do what I love. Thanks also to my friends who always make themselves available to have a beer and commiserate or celebrate. I couldn't have done it without you all.

Introduction

Climate change is rapidly altering the geographic distributions of species. Meta-analyses have suggested that species have been moving poleward at an average rate of between 6.1 km per decade (Parmesan & Yohe 2003) and 16.9 km per decade (Chen et al. 2011) in response to climate change. This has profound implications for the future of biodiversity as species are pushed into new habitats with their own sets of challenges for those species. In order to manage species with shifting distributions, it will be critical to understand where those future distributions might be. The primary method employed for predicting future range shifts are Species Distribution Models (SDMs) (Elith & Leathwick 2009). SDMs use occurrence data for a species, and combine it with data on climatic variables in order to determine the climatic envelope in which the species can survive. Once the climatic tolerances of the species are determined, projected climate data can be used to subsequently determine what habitat will be suitable for the species in the future.

There are many assumptions in this approach, however, that, when violated, can compromise the results of the SDM. One of these assumptions is that a species is in equilibrium with its environment (Guisan & Thuiller 2005; Elith & Leathwick 2009). Under that assumption, a species occupies all the space that climate variables allow it to occupy. However, we know that factors besides climate often affect species' distributions. One of the most important factors is the presence of interacting species (Pearson & Dawson 2003; Araújo & Luoto 2007; Wiens 2011; Suttle et al. 2007; Austin 2007). A species may not be able to coexist with another competing

species, or it may not be able to persist in regions that lack an obligate mutualist. Failure of SDMs to incorporate species interactions has been widely recognized as a major caveat to their predictive ability (Guisan & Thuiller 2005; Brooker et al. 2007; Godsoe & Harmon 2012; Giannini et al. 2013; Urban et al. 2013; Van der Putten et al. 2010). Studies that have incorporated species interactions into their models have found that they can drastically alter the predictions of SDMs under future climate scenarios, primarily by limiting the future potential ranges of species (Schweiger et al. 2008; Hof et al. 2012; Mason et al. 2014; Bulgarella et al. 2014).

A less discussed assumption of SDMs is that a species has one set of environmental tolerances, i.e. these tolerances are a species-level trait rather than a population-level trait. This assumption is made when a species is treated as a single group in an SDM, with all of its occurrence data belonging to that group. It is implicit in the name of the models, and nearly all SDMs have been created at the species level (Franklin 1998; Gottfried et al. 1999; Raxworthy et al. 2003; Morin et al. 2008; Williams et al. 2009; Wilting et al. 2010). This assumption, however, may mask ecologically relevant genetic differences within species that could influence predictions. We know that some species are composed of genetically distinct populations, which are often locally adapted to the climates they live in and the species they interact with (Avice 2000; Rehfeldt et al. 2002; Thompson 2005; Leimu & Fischer 2008; Valladares et al. 2014). Thus, a species may be comprised of several groups or populations, each with their own set of climatic tolerances. Moreover, each of these genetically distinct populations may coevolve with other species in different

ways, because each local interaction occurs in a unique abiotic and biotic environment. The result can be a geographic mosaic of coevolution in pairs or groups of interacting species (Thompson 2005; Thompson 2013). The interactions between any set of species are a composite of all the genetic differences and local adaptations and coadaptations they have accumulated across their geographic ranges.

Geographic mosaics in evolving interactions have implications not only for the ability of a species to persist or migrate in response to climate change, but also for the maintenance of genetic diversity and adaptive capabilities within a species, gene flow among populations, and the maintenance of local adaptation within populations. Different populations experiencing different magnitudes of climate change may expand their ranges into contact with other populations, or contract to further isolate themselves from other populations. These dynamics will likely affect the future ranges and abundances of species, as well as their ability to interact, form networks of interacting species, and create functioning ecosystems.

Because populations can be locally adapted to interacting species and populations, as well as abiotic factors, and the interacting populations and species are likely to change with climate change, the ecological outcomes of these interactions are also likely to be affected. As these populations move around, they may be forced to interact with species and populations with which they have not evolved. Predator-prey interactions could change as predators interact with new species or populations of prey to which they are not adapted, and vice versa (Harley 2011; Lehikoinen 2011). Likewise, plant-pollinator interactions could change as the balance between

cost and benefit for each partner changes with newly interacting species or populations.

Lineages of coevolving species may therefore be ideal systems for asking about the importance of incorporating species interactions and phylogeography into SDMs. These interactions may be particularly sensitive to climate change not only because climatic tolerances vary among each species, but because changes in the geographic mosaic of coevolving interactions may result in changes in the local ecological outcomes of these interactions. In the terminology of coevolutionary biology, the interactions show genotype by genotype by environment effects, where the ecological outcome of a species interaction differs depending on the environmental context in which it occurs. Such changes could affect both the persistence of the interacting species as well as the persistence of the interaction itself. In addition, the interdependence of coevolving species may make them more vulnerable to climate change, as a species that relies heavily on another needs to exist in a place that not only meets its own climatic requirements, but the climatic requirements of its interacting partner.

This study aims to answer the following two interrelated questions: (1) How much difference does incorporating species interactions into SDMs make in small, highly coevolved networks of interacting species, and what will those SDMs predict for the future of these species and interactions, and (2) How will incorporating phylogeographic information into these models affect our predictions for the future

distributions of these species, and what will be the consequences of climate-induced range shifts on this phylogeographic structure and interspecific genetic diversity?

Greya moths and *Lithophragma* plants comprise a very well studied small group of coevolving species, with a distinct geographic mosaic of interactions and species composition (Thompson 1997; Thompson & Cunningham 2002; Cuautle & Thompson 2010; Thompson et al. 2013). This highly specialized plant-pollinator interaction is ideally suited to asking the above questions because we have detailed information on which *Greya* species interact with which *Lithophragma* species across the range of the interaction, the ecological outcomes of these interactions in many populations, the molecular boundaries among *Lithophragma* species, and the phylogeographic structure of *Greya politella* (Prodoxidae) and *Greya obscura* (Thompson et al. 2013; Thompson & Fernandez 2006; Thompson et al. 2010; Kuzoff et al. 2001; Deng et al. 2015; Rich et al. 2008; Thompson & Rich 2011).

Methods

Study System

The coevolving interaction between *Lithophragma* plants and *Greya* moths, their pollinating seed parasites, is one in which there is nearly always mutual dependence. *Greya politella* and *Greya obscura* are wholly dependent on *Lithophragma* plants at every stage of their lives (Thompson & Rich 2011; Thompson & Fernandez 2006). Plants in five *Lithophragma* species differ among populations in the degree to which pollination depends on *Greya* moths, but *Greya* moths are the primary pollinators in most populations (Thompson & Fernandez 2006; Thompson et

al. 2013). All the *Lithophragma* species pollinated by *Greya* are self-incompatible in all populations that have been studied and therefore require pollination. Thus *Greya* moths specialized to *Lithophragma* cannot exist anywhere *Lithophragma* plants do not, and *Lithophragma* plants are probably very limited in their ability to disperse to areas that *Greya* moths cannot tolerate, as their seed sets would generally be very low. Since *Lithophragma* plants also reproduce asexually using bulbils, they may however be able to persist in areas lacking *Greya* moths for decades or longer. These dependencies among species must be accounted for if SDMs are to produce accurate predictions.

Both *G. politella* and *G. obscura* have a well-defined phylogeographic structure (Rich et al. 2008; Thompson & Rich 2011). *Greya politella* is a complex of four molecularly divergent subgroups that by some criteria may be considered cryptic species (Rich et al. 2008). Within *G. obscura*, there are three distinct diverging genetic subgroups, at least one of which may be a cryptic species (Thompson & Rich 2011). Previous work has demonstrated that there is also considerable variation among these subgroups in the species of *Lithophragma* they use as hosts, the way they use them, and the ecological outcomes of the interaction (Thompson & Cunningham 2002; Brown et al. 1997; Thompson et al. 2010). In addition, further such variation exists within these subgroups (Thompson & Cunningham 2002; Thompson & Fernandez 2006; Thompson et al. 2013). Thus, the phylogeographic groups provide conservative boundaries on the geographic scale of diversification with respect to both neutral genetic markers and adaptive traits. The ranges of each

Greya moth species as well as those of each subgroup are illustrated in Supplemental Figure 1.

The interaction between *Greya* moths and *Lithophragma* plants occurs in western North America from Baja California to British Columbia (Taylor 1965; Davis et al. 1992). The largest diversity of interacting *Lithophragma* and *Greya* species is found in the California Floristic Province (Davis et al. 1992; Thompson & Rich 2011). *Greya obscura* is found only in the California Floristic province, within a subset of *G. politella*'s range (Thompson et al. 2010). It is rarely found in populations that lack *G. politella*, and its persistence in some localities may rely on the superior pollination efficacy of *G. politella* (Thompson et al. 2013). Both *G. obscura* and *G. politella* pollinate *Lithophragma* plants, but they do so in different ways with very different efficiencies (Thompson et al. 2010). *Greya politella* may transfer some pollen when it nectars, but most pollination occurs when *G. politella* oviposit through the corolla of a *Lithophragma* flower, contacting both the anthers and stigma with their pollen-covered abdomens (Pellmyr & Thompson 1992). *Greya obscura* oviposit through the sepals or into the floral scapes, and therefore do not pollinate during oviposition (Thompson et al. 2010; Thompson & Rich 2011). They therefore pollinate only while nectaring. Because *G. obscura* oviposits into flowers, its larvae depend on the developing capsule and its seeds, and its persistence may rely upon the presence of *Greya politella* (Thompson et al. 2013).

Models

Occurrence data came from two sources. The first is a list of field surveys established by the Thompson Lab between 1999-2013 in which all species of *Lithophragma* and *Greya* present were noted. These surveys cover the vast majority of the range of the interaction between *Greya* and *Lithophragma*. The second consists of maps from the monograph on the biology and systematics of *Greya* Busck and *Tetragma* (Davis et al. 1992). The occurrence locations of *G. politella* and *G. obscura* on these maps were georeferenced using ArcMap 10.3 to obtain a list of GPS coordinates for those locations. See Supplementary Table 1 for sample sizes.

Climate data interpolated to 1 km resolution for 24 climate variables were sourced from ClimateWNA (Hamann et al. 2013; Wang et al. 2012). For current climate, we used data averaged over the period 1961-1990. For the future climate scenario, we used an ensemble model of 23 Atmosphere-Ocean General Circulation Models based on the CMIP3 climate predictions under the A2 (high emission) scenario for the 2080s. This scenario was chosen to analyze the potential maximum effects of climate on these species and interactions. All climate data were downloaded from <https://sites.ualberta.ca/~ahamann/data/climatewna.html>.

Species Distribution Models were then created in Maxent, version 3.3.3k, downloaded at <https://www.cs.princeton.edu/~schapire/maxent/> (Phillips et al. 2004; Phillips et al. 2006; Phillips & Dudík 2008). The random test percentage was set to thirty percent for all models, meaning that seventy percent of occurrences were used to train the models, and thirty percent to test them. All settings were left at their defaults except for the regularization coefficient, which controls how much the model

will be penalized for overfitting. The default is set to one, which, along with the other default settings, has been shown to be effective for many species (Phillips & Dudík 2008). When *Greya* and *Lithophragma* models were run with this regularization coefficient, however, the models of current niche space were overly generalized based on our knowledge of where they exist, and when visually compared with occurrence data accessed from the Global Biodiversity Information Facility, <http://www.gbif.org/>. Reducing the regularization coefficient to 0.5 produced models of current niche space that were more consistent with these sources, and thus this coefficient was used for all models in this study. In addition to running Maxent models for each species, we also ran individual models for the 4 genetic subgroups of *G. politella*, and 3 genetic subgroups of *G. obscura*. The geographic boundaries for these subgroups were determined from previous phylogeographic analyses (Rich et al. 2008; Thompson & Rich 2011). (See Figure S1 for the boundaries.)

The raw outputs of the Maxent models are heat maps of likelihood of occurrence over the specified range. Niche overlap among these raw outputs was calculated using ENMTools software, version 1.4.4, downloaded from <http://enmtools.blogspot.com/>. Two measures of niche overlap were calculated, Schoener's *D* and the *I* statistic, a version of Hellinger's distance modified to scale between 0 and 1 (Warren et al. 2008). The niche overlap between models of current and future ranges is a measure of similarity between current and future predicted distributions. Therefore, a smaller value for niche overlap represents a larger change in distribution over time.

We compared models further by making binary maps of habitat suitability in ArcMap 10.3 using a threshold value. The threshold used for each model was the 10 percentile training presence, which is the maximum threshold value that leaves ten percent of the known occurrences out of the predicted area under current climate conditions. Areas were calculated from these binary maps for comparison. The species interaction rules applied to the distributions were applied by overlaying and summing these binary layers, and using ArcMap 10.3 to calculate the areas of the summed regions. This method was also used to determine the network structure across the range of the interaction.

In order to ask how species interactions affected the results of the models, we compared these binary maps with and without several species interaction rules applied. The first rule was that *Greya* moths cannot exist anywhere that is not also suitable for *Lithophragma*. This rule is certainly the case, as *Greya* moths are completely dependent on *Lithophragma* plants at every stage of their lives (Thompson & Rich 2011; Thompson & Fernandez 2006). The models assumed that moths can use any *Lithophragma* species that have been recorded as hosts, as have been found during surveys for many studies over several decades (Schwind, pers. obs.; Thompson, pers. obs.). The second rule was that *Lithophragma* plants cannot disperse to places that are not suitable for *G. politella*. This is likely true most of the time, as most populations of the *Lithophragma* species included here are highly dependent on *Greya politella* for pollination, and thus reproduction by seed. Therefore, as soon as they move into habitat without *G. politella*, they will likely stop

dispersing. *G. obscura* has also been shown to do a non-trivial amount of pollination, but it is still far less effective a pollinator than *G. politella* (Thompson et al. 2010). The third rule only applies to the south Sierra Nevada population of *G. politella*. Experimental trials have shown that these moths have a unique method of pollinating *Lithophragma* flowers as they oviposit (Thompson et al. 2013). Rather than puncturing the nectar disk at the base of the corolla tube, they slide the ovipositor through a gap between the styles in the flower. The only *Lithophragma* species that has this gap is *L. bolanderi*, and so these moths may not easily switch to other *Lithophragma* hosts. Therefore, the third species interaction rule is that *G. politella* of the south Sierra Nevada population cannot exist anywhere outside of the predicted range of *L. bolanderi*. The fourth species interaction rule is that *G. obscura* cannot exist anywhere that *G. politella* is not present because its local persistence may depend on the superior pollination efficacy of *G. politella* to maintain sufficient *Lithophragma* seed sets and populations. Of these four rules, only the first is certainly true in all situations, but evaluating the models with and without each of these rules allows us to evaluate the extent to which detailed biological knowledge of an the interaction and the phylogeography of species affects the results.

Phylogeographic information was incorporated into the models by creating Maxent models for *G. obscura* and *G. politella* as one species each, and then separate models that treated each genetic subgroup as its own species. Binary maps were then created by the same protocol for each Maxent model so that areas of suitable habitat could be compared.

Analysis of network structure was performed by overlaying maps in Arc GIS. By doing so, we obtained the total area for each network configuration, i.e. how many moth species and how many plant species were present there. This analysis was done with both present and future predicted distributions so that we could predict the change in network structure over time.

Results

Models

Species varied widely in the extent that niche space changes over time, with the largest changes seen in *Greya obscura* and *Lithophragma campanulatum* (Fig. 1). These two species have the lowest niche overlap, based on Schoener's *D* and the *I* statistic (Table S1). The three species predicted to change the least over time are the three *Lithophragma* species that form a major clade within the genus, and are distributed in a ring around the Central Valley of California, *L. heterophyllum*, *L. cymbalaria*, and *L. bolanderi* (Kuzoff et al. 2001; Thompson et al. 2013).

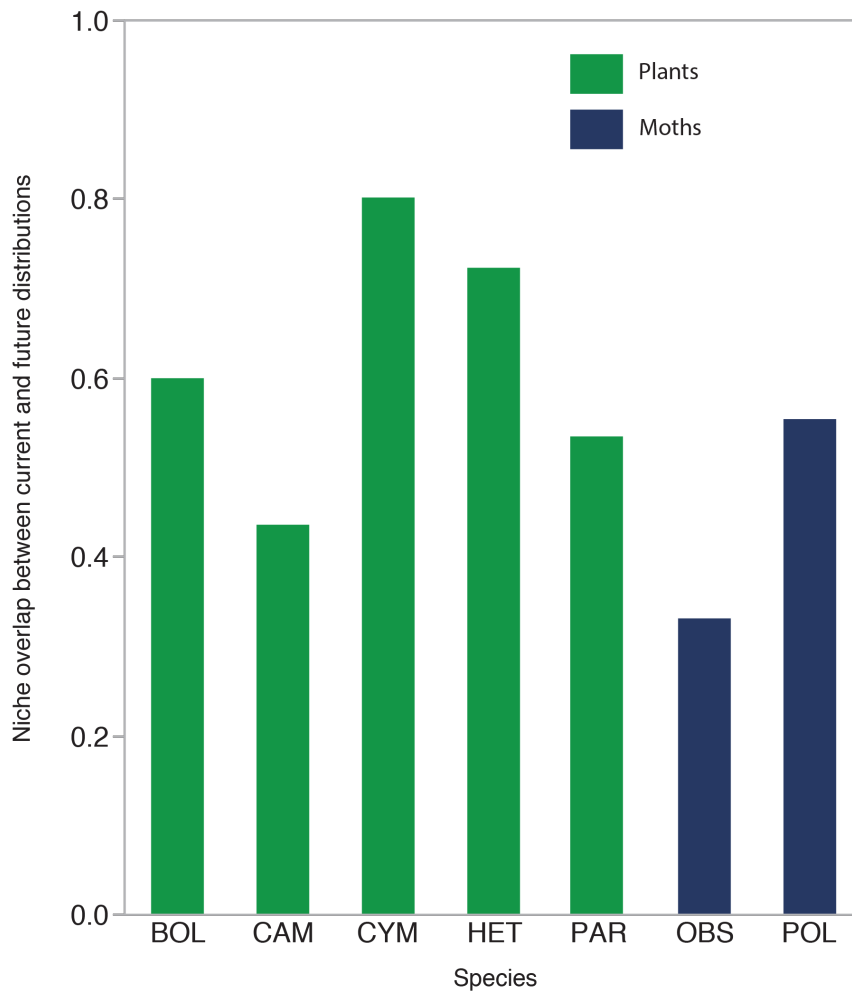


Fig. 1. Schoener's D values for niche overlap between maps of current and future predicted range maps for each *Lithophragma* plant and *Greya* moth species. Species designations are BOL=*L. bolanderi*, CAM=*L. campanulatum*, CYM=*L. cymbalaria*, HET=*L. heterophyllum*, PAR=*L. parviflorum*, OBS=*G. obscura*, POL=*G. politella*.

All species except *L. heterophyllum* showed increases in their niche space between now and the 2080s when dispersal was unlimited, species interactions were

not considered, and moth phylogeography was not incorporated (Fig. 2). The amount of niche space that these species gained was highly variable, however. *Lithophragma campanulatum*, *L. parviflorum*, and *G. politella* made extremely large gains when dispersal was allowed, whereas *L. bolanderi* and *G. obscura* made only relatively modest gains.

When dispersal was not allowed, species could only lose niche space over time, and they did so to varying degrees (Fig. 2). *Greya obscura* and *L. heterophyllum* 72% and 62% of their ranges, respectively, *G. politella* and *L. parviflorum* lost 38% and 42%, respectively, and *L. bolanderi* and *L. campanulatum* lost 9% and 8%, respectively. *Lithophragma cymbalaria* lost no niche space, meaning that all of its current range is predicted to still be suitable habitat in the 2080s under the A2 emissions scenario.

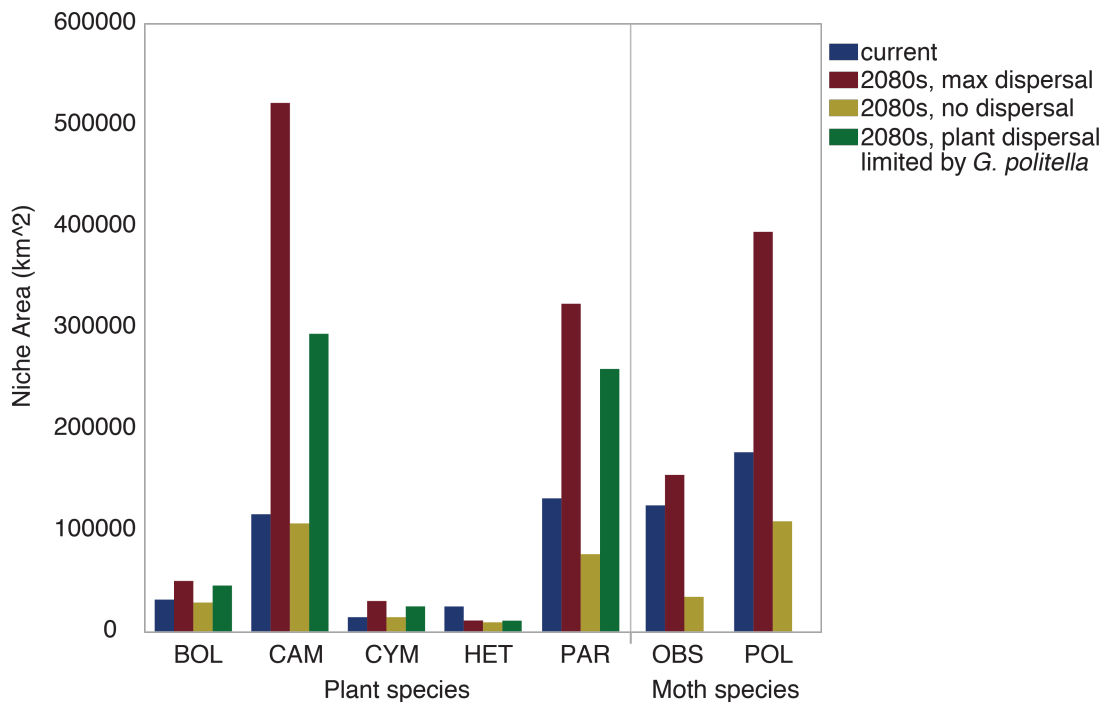


Fig 2. Areas of current and future niche spaces for all *Lithophragma* and *Greya* species under three and two dispersal scenarios, respectively. All species are shown under unlimited dispersal and no dispersal scenarios. Future *Lithophragma* ranges are also shown when their dispersal is limited to potential habitat for *G. politella*. Species designations are BOL=*L. bolanderi*, CAM=*L. campanulatum*, CYM=*L. cymbalaria*, HET=*L. heterophyllum*, PAR=*L. parviflorum*, OBS=*G. obscura*, POL=*G. politella*.

Species interactions

When limiting *Lithophragma* dispersal to places where *G. politella* also has future niche space, plant species differed greatly in their responses (Fig. 2). Reductions in future niche space ranged from 1.5% in *L. heterophyllum* to 43.6% in *L. campanulatum*. *L. parviflorum* and *L. cymbalaria* had considerable reductions at 19.9% and 17.3%, respectively, and *L. bolanderi* showed a 9.0% reduction.

Limiting future available niche space for *Greya* species to locations that were also suitable for *Lithophragma* constrained the niche space considerably for *G. politella*, but only slightly for *G. obscura*, which is already much more restricted geographically than *G. politella*. Future niche space for *G. politella* was constrained 18.5%, whereas *G. obscura*'s future niche space was constrained 3.9% (Fig. 3). If *G. obscura* is further limited to future available niche space for *G. politella*, its niche space is reduced another 26.2%.

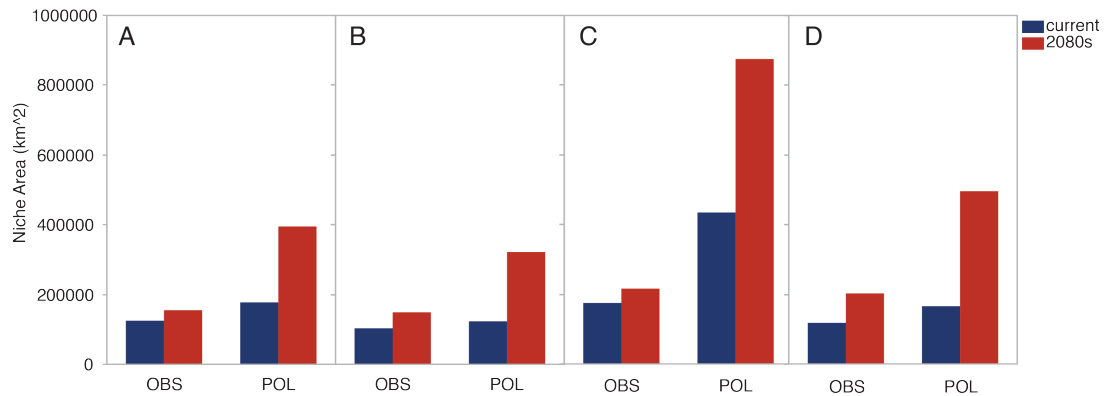


Fig. 3. Current and predicted future niche areas of *G. obscura* and *G. politella* under four scenarios: A) *G. obscura* and *G. politella* are treated as one species each and are not limited by the niche space of *Lithophragma*. B) *G. obscura* and *G. politella* are treated as one species, and are limited by the niche space of *Lithophragma*. C) *G. obscura* and *G. politella* are treated as three and four genetic subgroups, respectively, and are not limited by the niche space of *Lithophragma*. D) *G. obscura* and *G. politella* are treated as three and four genetic subgroups, respectively, and are limited by the niche space of *Lithophragma*.

Phylogeography

We next evaluated the effects of treating *G. obscura* and *G. politella* as three and four diverging genetic subgroups, respectively, and evaluating the total area of future niche space available to one or more cryptic species (Fig. 3). Under this scenario, the future niche space available to one or more subgroups of *G. obscura* or *G. politella* is much higher than the predictions of their ranges when considered just 2 species. The combined future niche space for the three subgroups of *G. obscura* covered a total of

216,068 km², 39% more than the predicted area for *G. obscura* when it is treated as one species. The combined future niche space for the four subgroups of *G. politella* is 874,718 km², 121% greater than when it is treated as one species. However, when moths are limited to where *Lithophragma* plants also have available niche space, these numbers are reduced. Under the three genetic subgroup scenario, *G. obscura* is predicted to have a niche space of 202,390 km² in 2080 when it is confined to future *Lithophragma* niche space, a 6.3% reduction. *G. politella*, under the four genetic subgroup scenario, is reduced 43.3% when it is limited to future *Lithophragma* niche space (Fig. 3).

Treating each genetic subgroup as a separate species in these models also allowed us to look at the fate of each subgroup individually in order to look at how climate change may affect genetic diversity within each species. The largest potential gains for both moth species are in their northernmost subgroups (Fig. 4). *Greya obscura* loses more than half of its range in the transverse ranges, and its tiny range in the south Sierra Nevada Mountains is reduced from 4593 km² to 3822 km². *G. politella* makes gains in all four of its genetic subgroups, but the largest gain by far is in the Pacific Northwest subgroup. The large increase in the niche space of *G. politella* when it is treated as four species instead of one is mostly due to this much larger range expansion in the Pacific Northwest. The south Sierra Nevada subgroup also gains a large percentage of niche space, increasing 225.7%. These gains, however, all still highly depend on these species' ability to disperse. If these moths are not able to disperse, many populations will lose a great deal of their current range

(Fig. 4). The fact that the northernmost populations lose considerable niche area if they cannot disperse, while also gaining large amounts of niche area if they can disperse, shows that these subgroups will depend heavily on suitable future habitat.

When the south Sierra Nevada populations of *G. politella* were considered as a subgroup that can only use *L. bolanderi* as a host, and were thus limited to future niche space that is also available to *L. bolanderi* in the future, their potential niche space was severely reduced. The predicted future area of niche space dropped from 91,451 km² to 26,574 km² (results not shown).

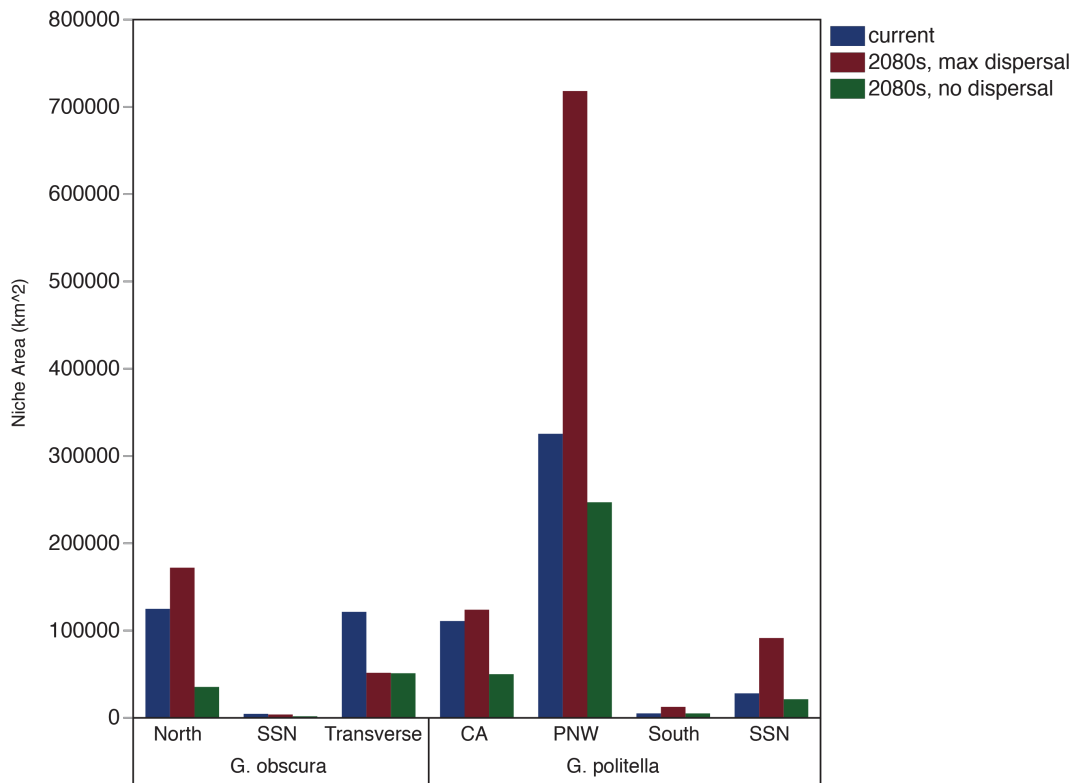


Fig 4. Current and predicted range sizes for each genetic subgroup of *G. obscura* and *G. politella* under an unlimited dispersal scenario and a no dispersal scenario.

Subgroup designations for *G. obscura* are North= Northern; SSN= South Sierra Nevada; Transverse= Transverse Ranges. Subgroup designations for *G. politella* are CA= California, PNW= Pacific Northwest, South= Southern; SSN= South Sierra Nevada.

Networks

The structure of networks across the landscape changed considerably by the 2080s in the models in which *Greya* moths were limited to locations with *Lithophragma*, *Lithophragma* had unlimited dispersal, and *G. obscura* and *G. politella* were treated as one species each. Since the ranges of both plant and moth species are almost all expanding, there was also an increase in almost all network configurations (Fig. 5). The only configurations that lost range area are those that have both moth species. Of these configurations, three of the four species lose range area (Fig. 5). The largest gains are for situations in which one *Lithophragma* species occurs without any moth species, which suggests there is considerable decoupling of plants and moths predicted in the models. When the network change is evaluated as proportional change (Fig. 6), the current network structure is split almost evenly among networks with no moths, one moth, and two moths. In the future scenario, however, networks lacking moths comprise nearly half of the total area, networks

with two moths are considerably reduced, and networks with one *Greya* species and 2 *Lithophragma* species show a large proportional gain in area (Fig. 6).

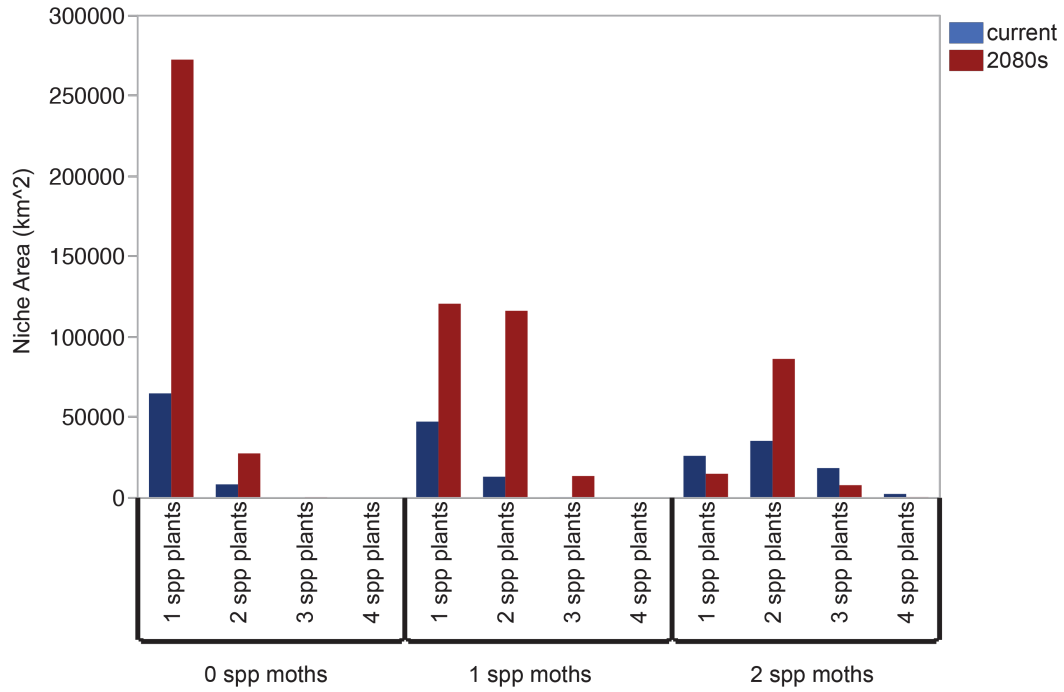


Fig. 5. Current and predicted future areas of each *Greya/Lithophragma* network configuration, assuming unlimited dispersal

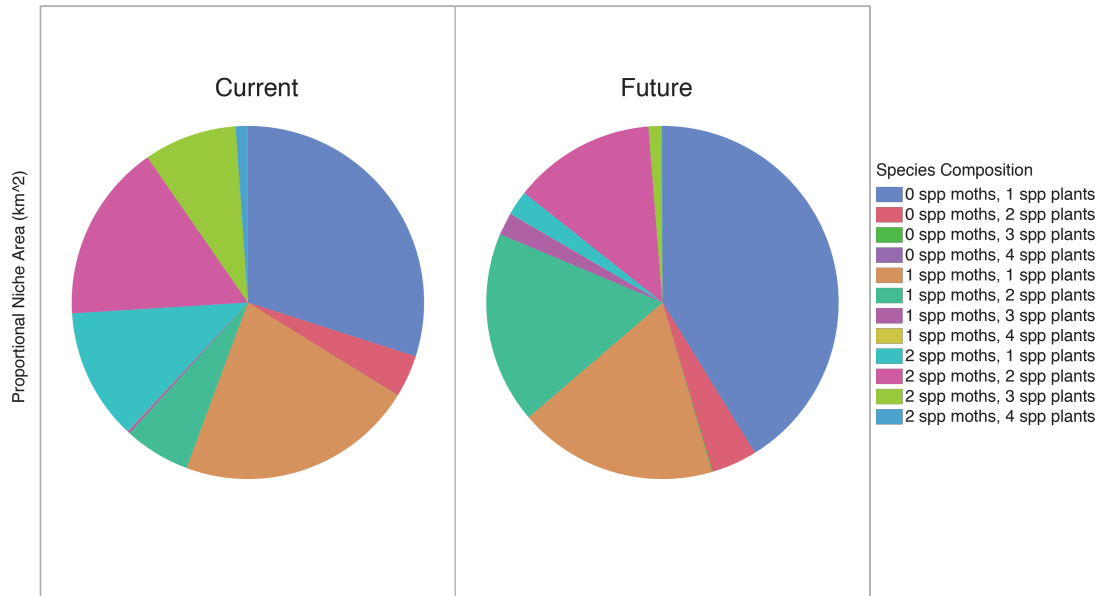


Fig. 6. Proportional changes in network structure across the range of the interaction between *Greya* moths and *Lithophragma* plants, assuming unlimited dispersal.

Discussion

This study highlights the importance of considering species interactions and phylogeography when evaluating Species Distribution Models. The five closely related *Lithophragma* plant species and two closely related *Greya* moth species all had very different responses to the incorporation of species interactions into the models. When *Lithophragma* spp. were limited in their dispersal to places that were also future suitable habitat for *G. politella*, their predicted future ranges were constrained by nearly half for *L. campanulatum*, but almost nothing for *L. heterophyllum*. The two *Greya* species also differed in their responses to limitations imposed by particular host species, which likely reflects differences in how their current ranges compare to the overall range of *Lithophragma*.

Recently, multiple studies have highlighted the need to incorporate species interactions into SDMs (Suttle et al. 2007; Schweiger et al. 2008; Wisz et al. 2013; Giannini et al. 2013). This study reinforces the importance of including species interactions, at least for coevolving species, by demonstrating that the predicted future ranges of plants of the same genus can differ widely even when responding to the same pollinator species. In the study system use here, where species interactions are limiting plants' dispersal, species whose future ranges are highly dependent on dispersal will be most heavily affected. The large future range of *L. campanulatum* depends heavily on dispersal, whereas the small and shrinking future range for *L. heterophyllum* depends less on dispersal. This is likely a more generalizable pattern for animal-pollinated perennial plants. Since plants can only disperse by reproduction, if animal-pollinated plants need to disperse a great deal in order to realize their future predicted ranges, they will be heavily dependent on their pollinators to do so. The situation is surely more extreme for annual plants. Since *Lithophragma* plants are perennials, they may be able to persist for some time in locations without their pollinators, but the future ranges of annual plants will be limited exclusively to locations that are also suitable for their pollinators.

Another way that plants may respond to climate change is to shift their phenology (Thuiller et al. 2008; Menzel et al. 2006; Bellard et al. 2012; Hegland et al. 2009). In many cases, this might cause a mismatch between flowering times of plants and the presence of their pollinators, causing limitations beyond the range limitations investigated in this study. However, in the case of *Lithophragma* and *Greya* moths, it

seems unlikely that a phenological mismatch would occur. The entire life cycle of *Greya* moths revolves around *Lithophragma* plants. Those studying these interactions have witnessed year-to-year variation in flowering times of as much as two weeks within local sites, with *Greya* moth adult emergence continuing to match flowering time closely in most years (e.g., Thompson and Fernandez 2006, Thompson et al. 2010). *Greya* moths in the lab eclose when the *Lithophragma* plants around them begin flowering, even when the calendar timing for their emergence is different from their timing in the field (pers. comm.). For these reasons, the possibility of future temporal mismatches was not considered in this study.

The differences in response of the moth species to models that incorporated species interactions were highly variable, but follow what is known of the relative range distributions of these species and their phylogeography. Since *Greya* moths depend completely on *Lithophragma* plants, their entire future range is limited to where there will be *Lithophragma* plants. Although the future predicted range of *G. obscura* is only slightly reduced by this limitation, *G. politella* is much more so. When *G. politella* is treated as four subgroups, the effect of this limitation increases considerably. Thus, not only are two species in the same genus affected very differently, but the same species treated under two phylogenetic scenarios is affected very differently in each scenario. This variability in the importance of incorporating species interactions into SDMs makes it difficult to predict when they may be important to consider. In the case of *G. obscura*, it turned out to make only a small difference, even though the moths are completely dependent upon the plants. One

explanation for the difference between *G. obscura* and *G. politella* here is that *G. obscura*'s current range is surrounded by a large buffer of *Lithophragma*, whereas *G. politella*'s current range edges push up against *Lithophragma*'s range edges. Thus, as *G. obscura* disperses, it is more likely to find *Lithophragma* in its newly colonized area. If *G. politella* is predicted to disperse in a slightly different direction than *Lithophragma*, then the two are likely to have less overlap in their predicted future ranges, and therefore *G. politella* would be more affected by the application of species interactions into its SDM.

The two interaction rules that represent the most detailed knowledge of the interaction were that *G. obscura* cannot be anywhere *G. politella* is not, and the south Sierra Nevada subgroup of *G. politella* is limited to using *L. bolanderi* as a host. Specifically, the oviposition method employed by the south Sierra Nevada subgroup of *G. politella* that limits it to using *L. bolanderi* as a host was discovered only by slicing small windows into the sides of *Lithophragma* flowers, and using time-lapse macro photography to observe oviposition behavior. This rule reduced the predicted range of south Sierra Nevada *G. politella* by over seventy percent. Both of these rules made considerable differences in the predictions of these models, underscoring the need for detailed understanding of species, populations, and the interactions among them, in order to make the best predictions of future ranges.

This study also highlights the importance of running SDMs at the appropriate phylogenetic level. While we do not know the phylogenetic level at which *Greya* moths are adapted to climate, running models for *G. politella* under two different

phylogenetic scenarios, both of which could represent the level of adaptation to climate, yielded very different results. Interestingly, the models for *G. obscura* showed relatively modest differences between the two phylogenetic scenarios. This difference may be related to the overall range of each species. Since *G. politella* is found in a much more diverse set of climates, these models may assume that the ideal conditions for the species are the average conditions across this space, with the moths at the range edges existing at the extremes of their climatic tolerances. If climatic tolerances are more locally adapted, however, it would make more sense to run these models at the genetic subgroup level examined here. When the models are run this way, the populations at the range edges are right in the middle of their climatic tolerances rather than at the extremes, and they are thus less likely to be as negatively affected by shifts in that climate. This interpretation would explain the much larger expansion of the northern population of *G. politella* when the models were run at the genetic subgroup level as opposed to when they were run at the species level. Since *G. obscura* occupies a much smaller range of climatic conditions currently, this effect should be much smaller, which it is in the models. This may be a useful generalization for future SDMs. Perhaps the larger a climatic niche a species occupies, the larger of a difference it will make to run SDMs at a lower phylogenetic level. Running SDMs at a lower phylogenetic level may be more appropriate when a species has a larger range as well. When a species exists in conditions that range from Baja California to British Columbia, it seems likely that the populations at those range edges would not have the same set of environmental tolerances.

Climate change is widely predicted to become a major driver of biodiversity loss over the coming century (Bellard et al. 2012; Thuiller et al. 2008; Thomas et al. 2004; Parmesan 2006; Cheung et al. 2009). While land use change is still considered the largest threat to biodiversity in terrestrial ecosystems, it is expected that climate change will increase considerably in its relative influence over the next fifty years (Sala et al. 2000; Thuiller 2007). It is increasingly recognized, however, that biodiversity loss will not only happen at the species level, but also at the level of intraspecific genetic diversity (Bálint et al. 2011; Habel et al. 2011; Taubmann et al. 2011; Pauls et al. 2013). Since this diversity may be critical to species' ability to adapt to a changing climate, preserving this intraspecific diversity may be vital for protecting species in the future.

This study examines what may happen to the intraspecific genetic diversity within each of the *Greya* species modeled. The *Lithophragma* species could not be analyzed in the same way because *Lithophragma* species show less evidence of clear phylogeographic divergence at the same spatial scale as *Greya*, based on currently available molecular results. When we run separate models for each genetic subgroup of *Greya*, we see that while the species may be predicted to increase in range considerably, the level at which the range of each subgroup changes varies a great deal (see figure 4). In the case of *G. obscura*, only one of the three genetic subgroups is predicted to gain range area over the time period investigated. This one subgroup gains more than the other subgroups lose, so the species is predicted to gain in range overall, but genetic diversity within the species is being lost. In the case of *G.*

politella, all genetic subgroups gain range area, but the vast majority of range area gained by the species is just one subgroup. Thus, the fates of the other subgroups are much less optimistic than an analysis at the species level suggests.

The composition of networks of interacting species can have large consequences for the ecological outcomes of those interactions, and the corresponding coevolutionary process between the interacting species (Benkman 1999; Bascompte & Jordano 2007; Thompson et al. 2010). This study examined the future network structure of *Greya* and *Lithophragma* species predicted by SDMs. Since the ranges of nearly all species examined increased over time, so did the range of most network configurations. However, the proportion of range currently occupied by each network configuration will change, as will the proportion of *Lithophragma* ranges lacking *Greya* moths. In the longer term, some *Lithophragma* populations lacking *Greya* would likely go extinct. It more difficult to evaluate the relative long-term persistence of *Lithophragma* populations with one rather than two *Greya* moth pollinators, but the proportional decrease in sites with both moth species may have negative consequences for *Lithophragma* as well. In one population of *L. cymbalaria* that interacts with *G. politella* and *G. obscura*, *G. obscura* has been shown to be an important contributor to pollination in a year with low numbers of *G. politella*, even though *G. obscura* is a relatively inefficient pollinators (Thompson et al. 2010). This result suggests that the system is stabilized by the presence of *G. obscura*. Thus, the proportional loss of two moth sites as well as the large proportional increase in zero moth sites is likely to place the long-term viability of these networks in jeopardy.

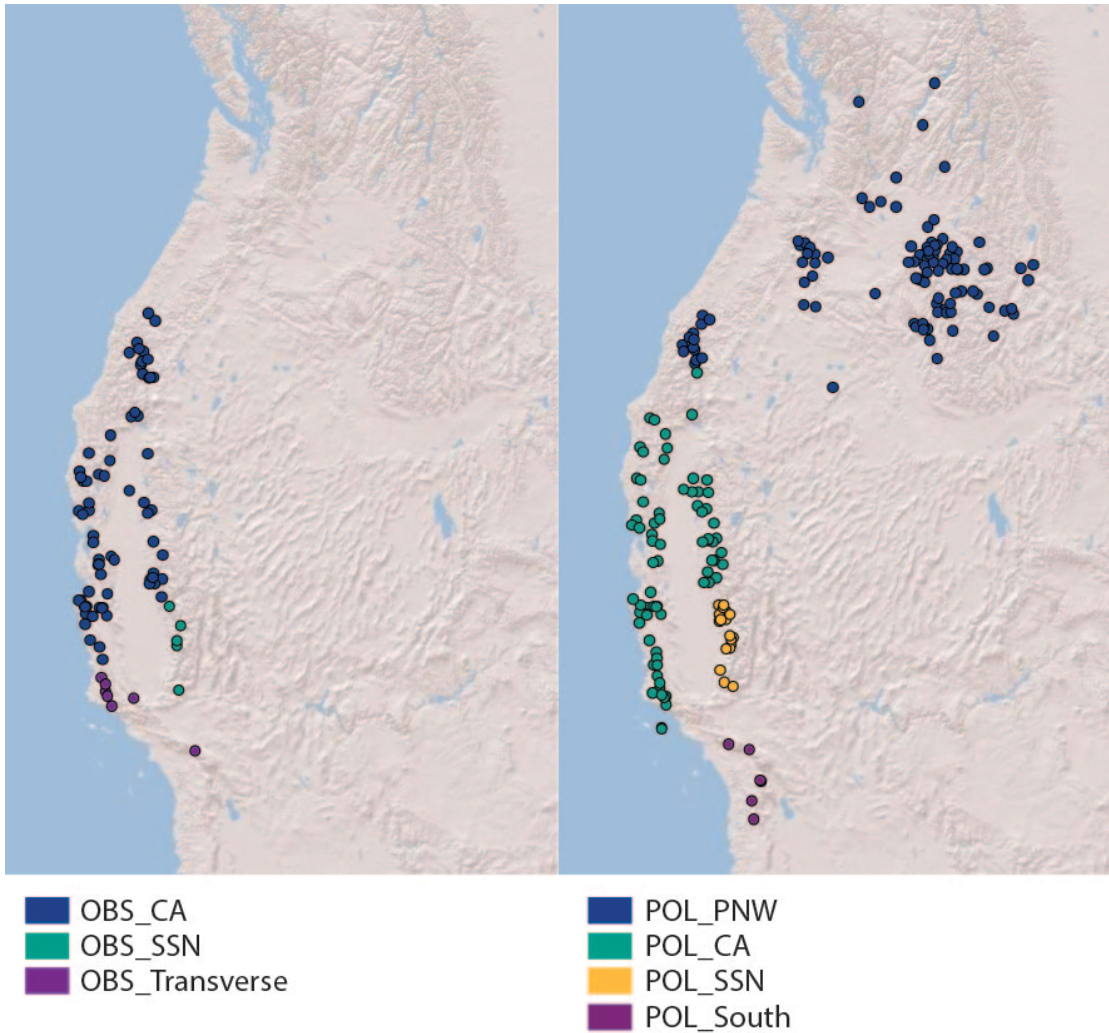
In conclusion, this study demonstrates that SDMs of groups of very closely related species can have very different responses to the incorporation of species interactions as well as the phylogenetic treatment of the species. SDMs remain the best tool we have to predict the future ranges of species, but their results may be very far from reality if they are not run at the appropriate phylogenetic level and the interactions they have with other species are not well understood. In addition, when considering the future of ecosystems, we must consider the future of species interactions in addition to the species themselves. These interactions are critical to ecosystem functioning, but are often not considered in SDMs. By considering how networks of interacting species change over time, we can predict how species interactions will react to climate change, in addition to the species themselves.

Supplemental Information

Species	N occurrences	Logistic threshold	% Overlap between current and future	I overlap between current and future	Schoener's D overlap between current and future
BOL	28	0.362	54.6	0.85	0.60
CAM	9	0.220	20.2	0.75	0.44
CYM	9	0.563	47.7	0.97	0.80
HET	29	0.451	35.3	0.93	0.72
OBS	82	0.318	14.1	0.62	0.33
PAR	131	0.451	20.3	0.81	0.53
POL	202	0.437	23.6	0.82	0.55
OBS_North	70	0.334	13.5	0.61	0.33
OBS_SSN	5	0.664	27.5	0.73	0.43
OBS_Transverse	7	0.334	41.9	0.97	0.83
POL_CA	73	0.343	27.1	0.77	0.48
POL_PNW	105	0.249	31.0	0.82	0.55

POL_South	6	0.652	40.4	0.96	0.80
POL_SSN	18	0.368	21.7	0.68	0.33

Supplemental Table 1. Sample sizes, thresholds, and overlap measures between current and future niches for each species and genetic subgroup of *Lithophragma* and *Greya*



Supplemental Figure 1. Assignment of *G. obscura* and *G. politella* moth populations to genetic subgroups. Subgroup designations for *G. obscura* are North= Northern; SSN= South Sierra Nevada; Transverse= Transverse Ranges. Subgroup designations

for *G. politella* are CA= California, PNW= Pacific Northwest, South= Southern, SSN= South Sierra Nevada.

References

- Araújo, M.B. & Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, 16(6), pp.743–753. Available at: <http://doi.wiley.com/10.1111/j.1466-8238.2007.00359.x>.
- Austin, M., 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, 200(1–2), pp.1–19.
- Awise, J.C., 2000. *Phylogeography: the history and formation of species.*, Harvard University Press.
- Bálint, M. et al., 2011. Cryptic biodiversity loss linked to global climate change. *Nature Climate Change*, 1(6), pp.313–318.
- Bascompte, J. & Jordano, P., 2007. Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 38(1), pp.567–593.
- Bellard, C. et al., 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4), pp.365–377.
- Benkman, C.W., 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *The American Naturalist*, 153(s5), pp.S75–S91.

- Brooker, R.W. et al., 2007. Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, 245(1), pp.59–65.
- Bulgarella, M. et al., 2014. Shifting ranges of two tree weta species (*Hemideina* spp.): Competitive exclusion and changing climate. *Journal of Biogeography*, 41(3), pp.524–535.
- Chen, I. et al., 2011. Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(August), pp.1024–1026.
- Cheung, W.W.L. et al., 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, 10(3), pp.235–251.
- Cuautle, M. & Thompson, J.N., 2010. Diversity of floral visitors to sympatric *Lithophragma* species differing in floral morphology. *Oecologia*, 162(1), pp.71–80.
- Deng, J. et al., 2015. Phylogeny, divergence times, and historical biogeography of the angiosperm family Saxifragaceae. *Molecular Phylogenetics and Evolution*, 83, pp.86–98.
- Elith, J. & Leathwick, J.R., 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), pp.677–697.
- Franklin, J., 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *Journal of Vegetation Science*, 9(5), pp.733–748.

- Giannini, T.C. et al., 2013. Improving species distribution models using biotic interactions: A case study of parasites, pollinators and plants. *Ecography*, 36(6), pp.649–656.
- Godsoe, W. & Harmon, L.J., 2012. How do species interactions affect species distribution models? *Ecography*, 35(9), pp.811–820.
- Gottfried, M. et al., 1999. A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Diversity and Distributions*, 5(6), pp.241–251.
- Guisan, A. & Thuiller, W., 2005. Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), pp.993–1009.
- Habel, J.C. et al., 2011. Global warming will affect the genetic diversity and uniqueness of *Lycaena helle* populations. *Global Change Biology*, 17(1), pp.194–205.
- Harley, C.D.G., 2011. Climate Change, Keystone Predation, and Biodiversity Loss. *Science*, 334(6059), pp.1124–1127.
- Hegland, S.J. et al., 2009. How does climate warming affect plant-pollinator interactions? *Ecology letters*, 12(2), pp.184–95.
- Hof, A.R., Jansson, R. & Nilsson, C., 2012. How biotic interactions may alter future predictions of species distributions: Future threats to the persistence of the arctic fox in Fennoscandia. *Diversity and Distributions*, 18(6), pp.554–562.
- Kuzoff, R.K., Hufford, L. & Soltis, D.E., 2001. Structural homology and developmental transformations associated with ovary diversification in

- Lithophragma (Saxifragaceae) 1. *American Journal of Botany*, 88(2), pp.196–205.
- Lehikoinen, A., 2011. Advanced autumn migration of sparrowhawk has increased the predation risk of long-distance migrants in Finland. *PLoS ONE*, 6(5).
- Leimu, R. & Fischer, M., 2008. A meta-analysis of local adaptation in plants. *PLoS ONE*, 3(12), pp.1–8.
- Mason, T.H.E. et al., 2014. Predicting potential responses to future climate in an alpine ungulate: Interspecific interactions exceed climate effects. *Global Change Biology*, pp.3872–3882.
- Menzel, A. et al., 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12(10), pp.1969–1976.
- Morin, X., Viner, D. & Chuine, I., 2008. Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology*, 96(4), pp.784–794.
- Parmesan, C., 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology Evolution and Systematics*, 37(May), pp.637–669.
- Parmesan, C. & Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), pp.37–42.
- Pauls, S.U. et al., 2013. The impact of global climate change on genetic diversity within populations and species. *Molecular Ecology*, 22(4), pp.925–946.
- Pearson, R.G. & Dawson, T.P., 2003. Predicting the impacts of climate change on the

- distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12, pp.361–371.
- Van der Putten, W.H., Macel, M. & Visser, M.E., 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365(1549), pp.2025–2034.
- Raxworthy, C.J. et al., 2003. Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, 426(6968), pp.837–841.
- Rehfeldt, G.E. et al., 2002. Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology*, 8(9), pp.912–929.
- Rich, K. a, Thompson, J.N. & Fernandez, C.C., 2008. Diverse historical processes shape deep phylogeographical divergence in the pollinating seed parasite *Greya politella*. *Molecular ecology*, 17(10), pp.2430–48.
- Sala, O.E. et al., 2000. Global Biodiversity Scenarios for the Year 2100. *Science*, 287(March), pp.1770–1774.
- Schweiger, O. et al., 2008. Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, 89(12), pp.3472–3479.
- Suttle, K.B., Thomsen, M. a & Power, M.E., 2007. Species interactions reverse grassland responses to changing climate. *Science*, 315(5812), pp.640–642.
- Taubmann, J. et al., 2011. Modelling range shifts and assessing genetic diversity distribution of the montane aquatic mayfly *Ameletus inopinatus* in Europe under

- climate change scenarios. *Conservation Genetics*, 12(2), pp.503–515.
- Thomas, C.D. et al., 2004. Extinction risk from climate change. *Nature*, 427(6970), pp.145–8.
- Thompson, J. & Fernandez, C., 2006. Temporal dynamics of antagonism and mutualism in a geographically variable plant-insect interaction. *Ecology*, 87(1), pp.103–112.
- Thompson, J.N. et al., 2013. Diversification through multitrait evolution in a coevolving interaction. *Proceedings of the National Academy of Sciences of the United States of America*, 110(28), pp.11487–92.
- Thompson, J.N., 1997. Evaluating the Dynamics of Coevolution Among Geographically Structured Populations. *Ecology*, 78(6), pp.1619–1623.
- Thompson, J.N., 2013. *Relentless Evolution*, Chicago: University of Chicago Press.
- Thompson, J.N., 2005. *The geographic mosaic of coevolution*, University of Chicago Press.
- Thompson, J.N. & Cunningham, B.M., 2002. Geographic structure and dynamics of coevolutionary selection. *Nature*, 417(6890), pp.735–738.
- Thompson, J.N., Laine, A.L. & Thompson, J.F., 2010. Retention of mutualism in a geographically diverging interaction. *Ecology Letters*, 13(11), pp.1368–1377.
- Thompson, J.N. & Rich, K.A., 2011. Range edges and the molecular divergence of Greya moth populations. *Journal of Biogeography*, 38(3), pp.551–563.
- Thuiller, W., 2007. Climate change and the ecologist. *Nature*, 448(August), pp.550–552. Available at: WOS:000248446700034.

- Thuiller, W. et al., 2008. Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, 9(3–4), pp.137–152.
- Urban, M.C., Zarnetske, P.L. & Skelly, D.K., 2013. Moving forward: Dispersal and species interactions determine biotic responses to climate change. *Annals of the New York Academy of Sciences*, 1297, pp.44–60.
- Valladares, F. et al., 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, 17(11), pp.1351–1364.
- Wiens, J.J., 2011. The niche, biogeography and species interactions. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 366(1576), pp.2336–50.
- Williams, J.N. et al., 2009. Using species distribution models to predict new occurrences for rare plants. *Diversity and Distributions*, 15(4), pp.565–576.
- Wilting, A. et al., 2010. Modelling the species distribution of flat-headed cats (*Prionailurus planiceps*), an endangered South-East Asian small felid. *PLoS ONE*, 5(3).
- Wisz, M.S. et al., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, 88(1), pp.15–30.

