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Community-level reorganizations following migratory pollinator dynamics along a latitudinal gradient

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Predicting how communities re-arrange in response to changes in species composition remains a key challenge in ecology. Migratory species, which enter and leave communities across latitudinal gradients, offer us a unique opportunity to evaluate community- and species-level responses to a shift in community composition. We focused on a migratory hummingbird and the communities that host it along a latitudinal and species diversity gradient. Our results show higher niche overlap in more diverse communities, allowing resident species to compensate for the loss of the migrant in providing pollination services. Contrastingly, in less diverse communities, the migrant behaves as a specialist, monopolizing abundant resources. In its absence, its role is not fully covered by resident species, resulting in a decrease in the fruit set of the migrant's preferred plant species. These results help us understand the potential impacts of biodiversity loss and have important implications for community persistence given expected changes in the migratory behaviours of some species.

1. Background

Ecosystems are suffering from the pressures of on-going global change, including climate change [1,2] and habitat loss [3]. One of the main consequences of ecosystem disturbance is the local extinction of species, yet we have little understanding of the consequences of these extirpations for ecological interactions, community dynamics and ecosystem functions. To predict how ecosystems, which are naturally dynamic, will react to these pressures, we first need to understand how communities react to the natural dynamics that lead to changes in their composition of species, with special emphasis on changes in species interactions and the ability of the community to re-arrange itself and maintain its functioning.

Up to now, understanding community-level rearrangements following changes in species composition has proved elusive, given the great complexity of ecological systems, which feature high levels of species diversity, interactions across species and environmental variability. The use of network analyses to represent some of the biotic interactions has allowed us to address part of this complexity [4,5]. However, many network studies have used temporally and spatially aggregated data of observed interactions representing a snapshot of a community [6–8]. Aggregating data omits important information regarding the dynamic nature of ecological interactions [6], and in particular concerning species functional roles, which can change due to competition for resources [9], the presence of parasites and pathogens [10] or changes in species composition [11]. These changes in species composition have been primarily assessed through studies focusing on species extinctions or invasions. Some of them have used

experimental set-ups to explore community level dynamics following species extinctions [11–13]. For example, Brosi & Briggs [11] temporarily removed the most abundant bumble-bee species and analysed how the rest of the pollinator community responded. They found that in manipulated sites, floral fidelity decreased, with consequences for plant reproductive success, and also that the loss of a single pollinator species changed pollination network structure [12]. One unresolved question is whether communities harbouring different diversity levels might respond differently. In other words, does biodiversity have a modulating role in these responses to changing species composition? We need to remove the same species from different background communities to see how responses differ across a diversity gradient. Given the complexity of these experiments, it is easy to see why such studies are not commonly done.

Migratory species and the communities that harbour them represent an ideal natural experiment in which the same species temporarily leaves ecosystems across latitudinal and diversity gradients. We surveyed communities of plants and the hummingbirds that pollinate their flowers along a latitudinal gradient from central Mexico to southern Alaska. We focused on communities that harbour the migratory rufous hummingbird *Selasphorus rufus*, and evaluated the foraging niches and the functional role of hummingbirds in the presence and the absence of the migratory species. We further explored the consequences of the removal of this species for plant reproductive success. Our study aims to answer three main questions. (1) How does the role of a single pollinator species change throughout its distribution range? (2) How do the roles of the rest of the hummingbird pollinators in the community change in response to a temporary species loss? (3) What are the consequences for the functions they perform? Given its widespread distribution, we expect that the migratory hummingbird will be a generalist species feeding on a diverse set of resources across all the range. Further, we expect resident species to change their feeding preferences when the migratory species is present or absent. In particular, we expect them to specialize on a small set of resources in the presence of the migratory competitor and then to expand their diet in its absence. Finally, we expect there to be changes on reproductive success particularly for those species of plants on which resident species specialized during the period in which the migratory species was present, but that will potentially receive heterospecific pollen during the period in which the migrant is absent as a consequence of an expansion in the diets of resident hummingbirds following [11].

2. Methods

(a) Study species and sites

Selasphorus rufus (Gmelin, 1788), the rufous hummingbird, undertakes spring and autumn migrations between wintering areas in central Mexico and breeding areas in southern Alaska and Canada [14]. We evaluated whether the functional role of this species changes within three communities along its migratory route: western Mexico, central California and southern Alaska, USA. In addition, at two sites (California and Mexico), we were able to compare time periods when the migratory species was present and absent to evaluate how the loss of one species changes the functional roles of the remaining species, with implications for plant reproductive success.

Las Joyas Biological Station is a 1245 ha natural reserve located in the Sierra de Manantlan within the states of Jalisco and Colima in Mexico (19°35′ N; 1040°16′ W, at 1952 m.a.s.l). Las Joyas experiences a mean annual temperature of 14.6°C and mean annual precipitation of 1610 mm, concentrated between June and October. The area hosts a complex mosaic of vegetation, including pine–oak forests, coniferous and cloud forests [15].

Landels-Hill Big Creek Reserve (36°4′0″ N 121°35′0″ W, 0–1,067 m.a.s.l) is a 1752 ha natural reserve in the Santa Lucia Mountains along the Big Sur coast in California. Big Creek Reserve experiences a mean annual temperature of 12.8°C and mean annual precipitation of 620 and 1020 mm at coast and upper peaks, respectively, concentrated between November and March. Vegetation includes an heterogeneous mixture of coastal scrub, redwood forests, coastal grasslands, oak woodlands and pine-oak forests [16].

In the area of Prince William Sound, Alaska, we conducted surveys at either side of the sound, at the localities of Valdez and Seward (61°07′50.99″ N −146°20′53.99″ W and 60°06′15.34″ N −149°26′36.60″ W and 30 and 0 m.a.s.l. respectively). Average precipitation in this area is 1520 mm while mean annual temperature is 5°C. Vegetation includes a mixture of closed needleleaf forest of mountain helmock, Sitka spruce, red and yellow cedar and open heath and bog areas.

(b) Hummingbird and plant surveys

Surveys were carried out during the year 2019. At each site, we selected six 1 km transects separated by at least 500 m from each other. Each transect was surveyed seven times per period during two periods: when the migrant species was present (January in Mexico, March in California and June in Alaska) and again after the migrant departed (April in Mexico and April–May in California). Between three and four transects were surveyed per day. The time at which transects were carried out was randomized every day. No surveys were done in Alaska during the absence period as no resident hummingbirds occur in this area. Along each transect, we recorded all the feeding interactions observed between every species of hummingbird present in the study area and every flowering plant species. In addition, we recorded flower availability of the different hummingbird-visited plants once for each period as the total sum of flowers observed per species.

In addition, in order to evaluate the impact of species removal on plant reproductive success, we further recorded several measures of plant reproductive success for a subset of plant species that were flowering in both periods: four in Mexico (*Fuchsia encliandra*, Onagraceae; *Lobelia laxiflora*, Lobeliaceae; *Rubus adenotrichos*, Rosaceae; and *Salvia iodantha*, Lamiaceae), and three in California (*Ribes sanguineum* and *Ribes menziesii*, Grossulariaceae; and *Castilleja affinis*, Orobanchaceae). These plants were selected because they were preferred resources by hummingbirds in the area and because they had two flowering periods, one when the migratory species was present and one in its absence. In Mexico, we counted the total number of seeds per fruit and measured fruit length and width in 30 fruits from five individuals per plant species. In California, we recorded fruit set for 10 individuals per plant species (only four individuals in the case of *Ribes menziesii*). For two of the species (*Ribes sanguineum* and *Ribes menziesii*), given the large number of flowers produced, we marked three branches within each of the 10 individuals per species and counted the number of flowers and three weeks later the number of fruits produced at each of the two periods (migrant present and absent). For the third species, *Castilleja affinis*, we recorded fruit set for the whole plant. In addition, we measured fruit length, width and wet weight for a subset

of 10 fruits per branch for each of the two *Ribes* species and for all fruits for *C. affinis* individuals.

(c) Species functional roles and interaction networks

To determine species functional roles, we extracted a series of metrics from plant–hummingbird interaction networks. For each transect within each period, we constructed a weighted bipartite interaction network [17] by pooling the data for the seven rounds of sampling. We then calculated a series of relevant metrics for the whole hummingbird community and for each of the hummingbird species in particular.

(d) Community-level metrics

At the community level, we focused on two metrics that provide parallel information on niche occupancy for the hummingbird guild. First, we calculated niche overlap using Horn's index [18], which estimates the similarity in interaction partners between hummingbird species. Second, we calculated functional complementarity. This metric, not correlated with the previous one (electronic supplementary material, table S1), presents additional information on the diversity of roles or niches occupied by hummingbird species. It is calculated as the total branch length of a functional dendrogram based on the Euclidean distance between hummingbirds in plant assemblages visited [19,20].

(e) Species-level metrics

At the species level, we focused on metrics that provide information on the functional role of each hummingbird species within the community. In particular, we calculated normalized degree, species-level specialization (d') and strength for each species at each transect and period. Normalized degree gives an idea of the diversity of plant species visited by each hummingbird species. It is calculated by dividing a hummingbird species' degree by the total number of plant species. In this case, we used the total number of flowering plant species found within our independent flower availability surveys as the denominator. d' provides information on the level of specialization of each hummingbird species based on discrimination from a random selection of partners [21]. In calculating this metric, we included abundance data as the flower availability for each plant species from our independent surveys. Strength provides complementary information on the dependence of plant species on a particular hummingbird species. It is calculated as the sum of the dependencies on that species of the plant species visited by a focal hummingbird [22]. All network metrics were calculated using package bipartite [17].

(f) Data analyses

First, we evaluated sampling completeness within our study by estimating the asymptotic number of plant and pollinator species present, as well as plant–pollinator links [23]. This is a non-parametric estimator of species richness for abundance data which includes non-detected species (or links), allowing us to calculate the proportion of species (or links) detected with our original sampling data. We used Chao 1 asymptotic species richness estimators [23] and estimated the richness of pollinators, plants and plant–pollinator links accumulated as sampling effort increased up to 100% sampling coverage using package iNEXT [24] within the R environment [25].

Then, to answer our first question related to how the role of a single species changes throughout its distribution range, we evaluated how the migratory species's normalized degree changed along its migratory pathway by fitting a general linear model including site as the explanatory variable.

In addition, we focused on changes in the role of migratory species through the indirect interactions it engages in by using motif analyses [26]. To this end, we compared the motif role signatures of *S. rufus* in Mexico and California (Alaska was not included in this analysis as there is only one hummingbird species there). Additionally, we compared the signatures of *S. rufus* to those of two other abundant species, *Hylocharis leucotis* in Mexico and *Calypte anna* in California. Motif role signatures were calculated using package bmotif [27]. Motif frequencies were normalized by dividing the position counts for each node by the total number of times that node appears in any of the positions [27]. Statistical comparisons were done using permutational multivariate analysis of variance (PERMANOVA) using Bray–Curtis as the dissimilarity distance. Visual comparisons were done by means of non-metric multidimensional scaling plots.

To answer our second question, related to how the roles of the other hummingbird species in the community shift when the migratory species is removed, we ran analyses at the whole community and at the species level. At the community-level, we evaluated whether niche overlap and functional complementarity varied across periods by running general linear mixed models (GLMMs) with period, plant species richness and floral resource availability as explanatory variables, and transect nested within site (California and Mexico) as a random factor. At the species level, we evaluated whether normalized degree, d', and strength varied across periods by running GLMMs that included period and its interaction with hummingbird species as explanatory variables. Transect nested within site was included as a random factor. For these species-level analyses, we removed the migratory species to focus on how the roles of the rest of the species change.

Finally, to answer our last question related to how changes in community structure and species functional roles might affect plant reproductive success, we ran separate GLMMs for the two sites (Mexico and California) as we were able to collect different measures of reproductive success. In the case of Mexico, response variables were fruit length, fruit weight and the number of seeds per fruit, scaled prior to analysis (i.e. we subtracted column means and divided by standard deviation) to allow meaningful comparisons across species with contrasting life histories. For California, response variables were fruit set, fruit length, width and weight. In both cases, models included period (migratory species present or absent) and its interaction with plant species as well as the plant's normalized degree, a measure of the diversity of pollinators visiting it, as explanatory variables. Plant individual was included as a random factor. We used a normal distribution to fit all models except in the case of fruit set where data were fitted to a binomial distribution. All statistical analyses were done using R [25] and all GLMMs were fitted using package lme4 [28].

3. Results

An analysis of the completeness of our sampling revealed that with our survey we were able to capture very high levels of hummingbird and plant species diversity at all sites ranging from 88 to 100% in hummingbird species, 56–100% in plant species and 55–100% in plant–hummingbird interactions (electronic supplementary material, figure S1).

As demonstrated by our analysis of foraging niches for the migratory hummingbird, the role of the migratory species *S. rufus* changed substantially throughout its distribution range. In particular, normalized degree, a measure of the number of plant species visited divided by all possible plant species, is much smaller in California than in either Alaska or Mexico (figures 1 and 2*a*). However, the difference is only
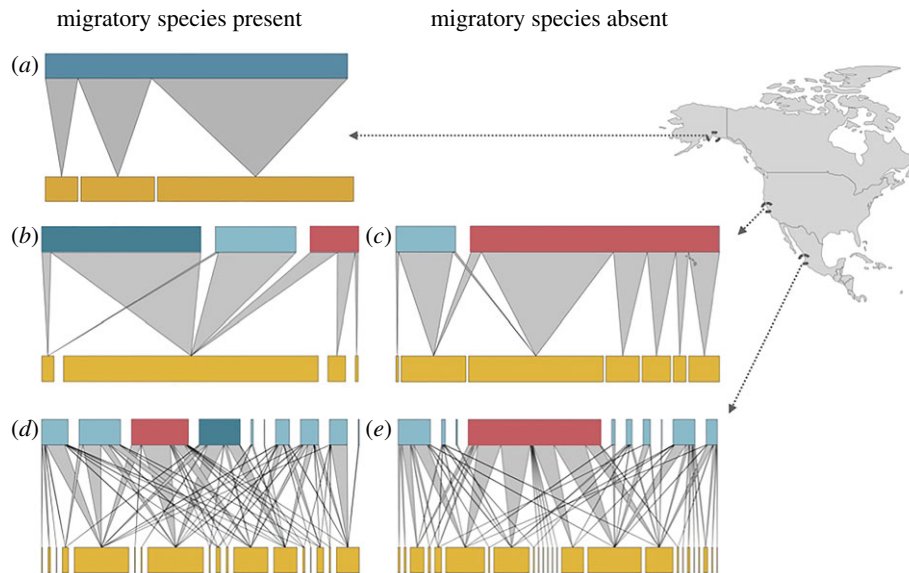
Figure 1. The structure of interaction networks between plants and hummingbirds at three sites across a latitudinal gradient: (*a*) Alaska, (*b*,*c*) California and (*d*,*e*) Mexico. (*a*), (*b*) and (*d*) show periods when the migratory species is present, and (*c*) and (*e*) show periods when it is absent. Upper polygons represent humming-bird species: light blue, resident species; dark blue, migratory species. Flagged in red are the two species that show largest changes between the two periods, *Calypte anna* in California and *Hylocharis leucotis* in Mexico. Lower yellow polygons represent plant species. (Online version in colour.)
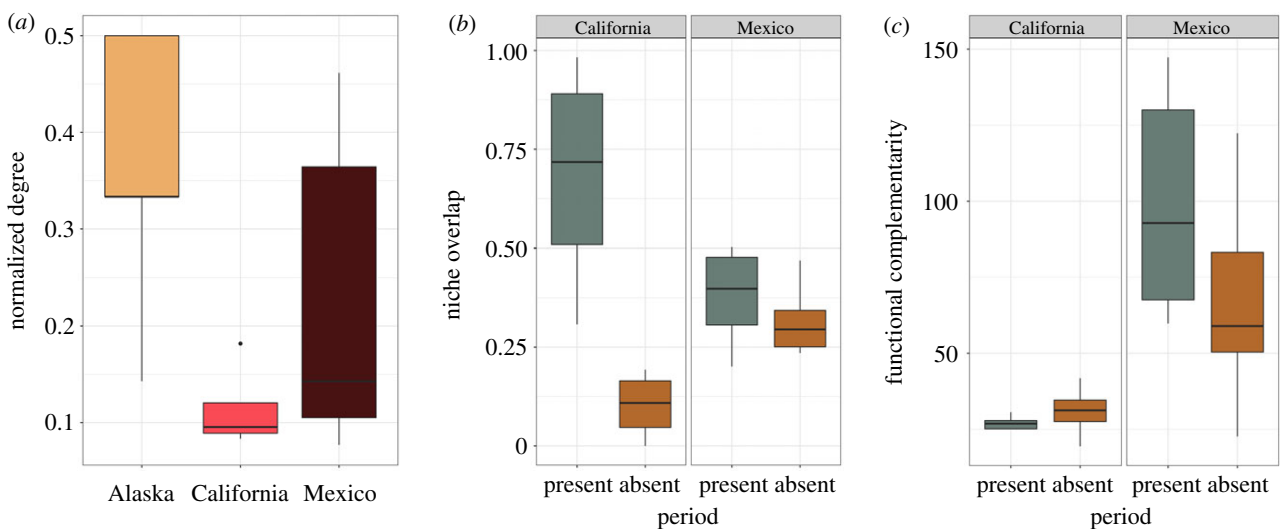

Figure 2. Boxplots showing (*a*) normalized degree for the migratory species *Selasphorus rufus* at three sites along its migratory pathway, and (*b*) how pollinator niche overlap and (*c*) pollinator functional complementarity change across periods (migratory species present–absent). Greater values indicate higher levels of generalization. (Online version in colour.)

significant between California and Alaska (z-ratio = 2.64, $p < 0.01$, marginal $R^2 = 0.32$), because inter-transect variability is high in Mexico. Despite there being a similar number of available plant resources in California and Alaska (three to four species), in California the migratory species feeds almost exclusively on one resource, *Ribes sanguineum*.

Our motif approach analyses to species roles shows that *S. rufus* has very different roles at two of the locations sampled (electronic supplementary material, figure S2A; $F = 6.43$, $p < 0.001$). While the species occupies mostly specialist roles in California, in Mexico it engages in interactions involving more than one plant species (electronic supplementary material, figure S2A). When comparing the role of the migrant species with that of two abundant species at each of the sites, *Hylocharis leucotis* in Mexico and *Calypte anna* in California, our results show a certain overlap between *S. rufus* and each of the two species when they co-occur ($F = 7.12$, $p < 0.001$),

while the overlap of their motif signatures is smaller in the absence of the migratory species.

In relation to the response of the hummingbird community to species removal, we focused our analyses on two different levels: at the level of the whole community and at the level of each of the hummingbird species. At the community level, when the migratory species leaves the area the niche overlap between different resident species decreases (figure 2*b*; marginal $R^2 = 0.31$). This effect is greatest in California (table 1*a*). In addition, we find that functional complementarity (i.e. niche complementarity of the hummingbird species) decreases in Mexico when the migrant leaves (table 1 and figure 2*c*; marginal $R^2 = 0.37$).

At the species level, all three variables evaluated change between periods before and after the removal of the migratory species. However, resident hummingbird species vary strongly in the magnitude and direction of these changes (figure 3;

Table 1. Results of GLMMs showing the effect of period (migratory hummingbird species present or absent) on resident community (*a*) niche overlap and (*b*) functional complementarity. Italics indicate variables with large and significant effects.

	estimate	s.e.	*t*-value
(*a*) niche overlap			
(intercept)	0.39	0.12	3.34
period	*−0.18*	*0.07*	*−2.51*
plant species richness	−0.01	0.01	−0.47
floral availability	0.00	0.00	0.37
(*b*) functional complementarity			
(intercept)	12.58	21.21	0.59
period	*−18.82*	*8.19*	*−2.30*
plant species richness	*6.75*	*2.69*	*2.52*
floral availability	0.00	0.00	0.08

electronic supplementary material, figure S3). In the case of California, we see particularly large changes in these variables for the species *Calypte anna*, which becomes more generalized (larger *d′*; electronic supplementary material, figure S4; model marginal $R^2 = 0.5$) and more important for the plant species that depend on it (greater strength, model marginal $R^2 = 0.52$) in the absence of the migratory species. In Mexico, the species whose role changes most is *Hylocharis leucotis*, which also diversifies the number of plant species it visits (larger normalized degree, model marginal $R^2 = 0.53$) and becomes more important for plant species in the community (greater strength) in the absence of the migratory species (figure 3).

As for our third question regarding the effect of species removal on plant reproductive success, the loss of the migratory hummingbird is associated with negative effects in California and positive effects in Mexico (electronic supplementary material, figure S5). In the case of California, *Ribes sanguineum* shows decreased fruit set after the loss of the migratory hummingbird (figure 4*b*; model marginal $R^2 = 0.24$), and all three plant species show slightly decreased fruit weight (electronic supplementary material, figure S8; model marginal $R^2 = 0.03$). *Castilleja affinis* shows a decrease in fruit length (model marginal $R^2 = 0.64$) and width (model marginal $R^2 = 0.64$) with loss of the migrant hummingbird (electronic supplementary material, figures S9 and S10).

By contrast, in Mexico the number of seeds per fruit increases with the loss of the migratory species for three of the four plant species sampled (electronic supplementary material, figure S5; figure 4*a*, model marginal $R^2 = 0.29$). In addition, two of the species show an increase in fruit length and fruit width (electronic supplementary material, figures S6 and S7, marginal $R^2 = 0.87$ and 0.93, respectively).

4. Discussion

Our results show that the foraging niches and functional roles of individual hummingbird species are dynamic and shift across their distribution areas. In particular, in the case of *S. rufus* its role changes from generalist to highly specialist in the community, and these niche shifts have a direct effect on its effectiveness as a pollinator. Moreover, our results

prove that the temporary local removal of a species can lead to important changes in the functional roles covered by the remaining species, and that these changes have an effect on the functions they perform. Here, we see the greatest changes in the niches occupied by one hummingbird species in Mexico (*H. leucotis*) and one in California (*C. anna*). In both cases, the species expand their niches and become more important in the community (greater strength values and thus greater dependence of plants on them) with the loss of the migrant from the community. However, these changes entail different consequences across the biodiversity gradient. In Mexico, the larger diversity of hummingbird species allows for another species (*H. leucotis*) to take over the role of the lost migrant, maintaining and even improving on the function performed by the latter. Conversely, in California, where hummingbird species diversity is lower, the role of the migratory species is not fully covered in its absence, leading to a reduced function.

Previous experimental research has suggested that species' functional roles shift in response to changes in community composition with differing consequences for the functions performed [11,13]. While Brosi & Briggs [11] found a negative effect of the loss of an abundant bumblebee for the reproductive success of *Delphinium barbeyi* (Ranunculaceae), Hallett *et al.* [13] found that the exclusion of bumblebees did not compromise the success of *Asclepias verticillate* (Apocynaceae). In this second case, the role of the lost species was taken over by another species (*Polistes* wasps). However, these studies, although highly valuable, were both carried out at small spatial scales and for relatively short periods of time, and focused on the reproductive success of just one species of plant. By contrast, our use of migratory species as a proxy for species loss allows us to evaluate the consequences of whole-landscape removals of the same species on natural communities along latitudinal gradients and to focus on the consequences for a larger subset of the plant species in the community. Of course, the continental scale of our approach and the fact that we have data for just 1 year also present some caveats, such as the confounding effect of latitude and diversity. By using a landscape-level natural removal of a species, we are able to show how species loss has large negative effects on some plant species, no effect on others, and in some cases produces effects that are over-compensated by changes in the roles of remaining species. Although our systems is not exactly a replica of a species extinction, since the communities we study have evolved with the presence of this migratory species, it clearly shows that understanding the consequences of species loss for ecosystem persistence requires of a community-level approach that focuses on the combined responses of multiple species and that takes into account the possible behavioural changes of the remaining species.

Our results provide evidence of the role of biodiversity as insurance against species loss [29]. As the migratory species disappears, we find that in the more diverse community the functions it performs are covered by other species that compensate for the loss and even improve the function of the lost species, thus ensuring the stability of the system. However, in the less diverse community, lower hummingbird diversity precludes the function of the migratory species from being covered by other hummingbird species and leads to a greater than 10% decrease in the reproductive success of the migrant's preferred plant species. It is important to note that although the species *Hylocharis leucotis* seems to take
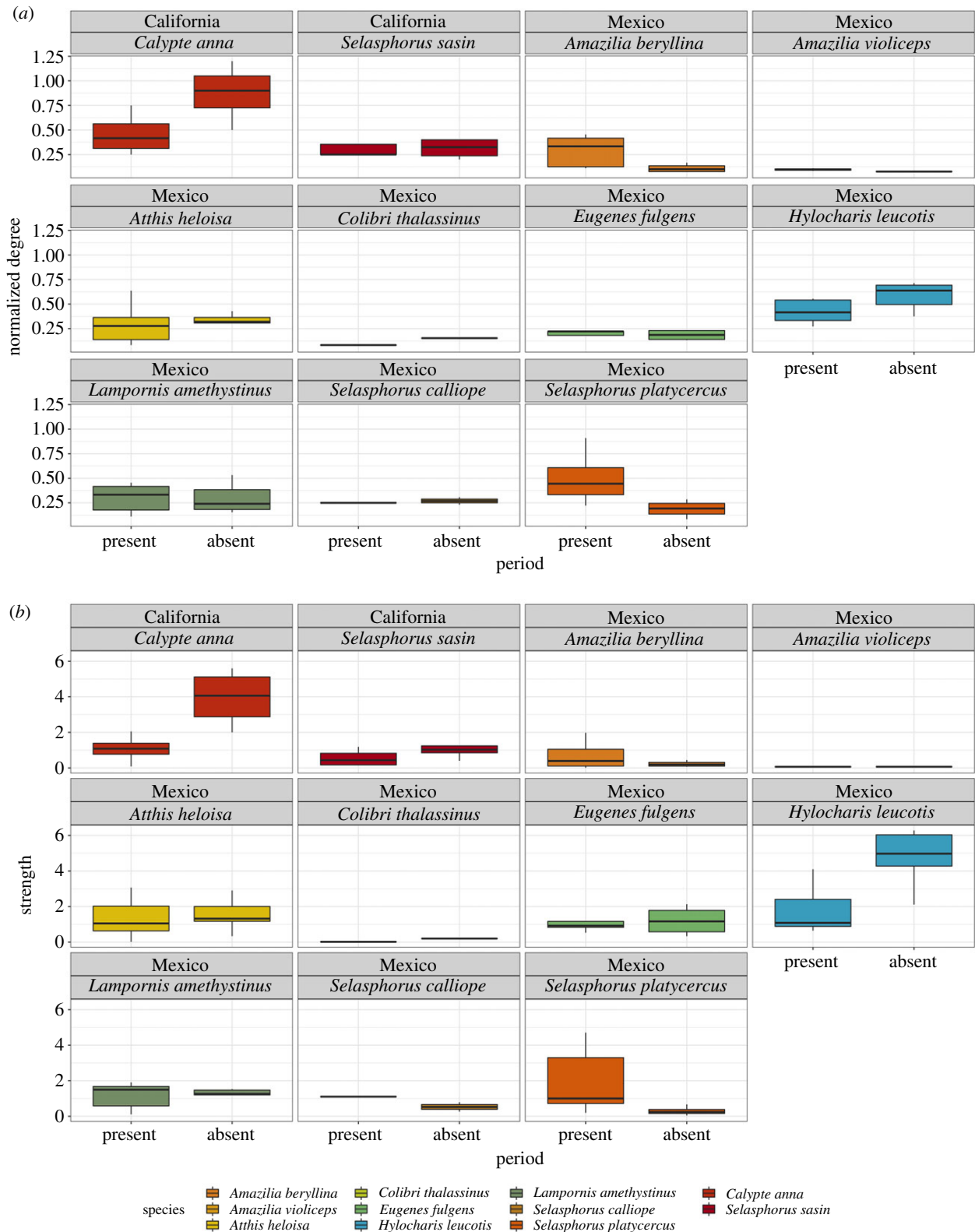
Figure 3. Boxplots showing how species-level metrics (*a*) normalized degree and (*b*) strength change across periods (migratory species present–absent) for each of the resident hummingbird species in the community. (Online version in colour.)

over the role as pollinator for most plant species visited by *S. rufus* in its absence, our analyses of the motif signatures of both species show some disparities suggesting that the resident species is not fully able to cover the role of the migrant. Nevertheless, the functional consequences of changing the indirect interactions captured by motif analyses are still far from being fully understood.

Insect pollinators, present during both periods, may also be important pollinators in these systems, yet their activity

is apparently not able to compensate for the loss of this one species from our observations. However, including insect species would have allowed us to evaluate the structure of the whole network of interactions involving plant species which could potentially reveal interesting results.

We also show how this species's foraging niche can dramatically change along its distribution range. In particular, we find that *S. rufus* behaves as a more generalist species at its wintering and breeding areas, while it becomes a specialist during part of
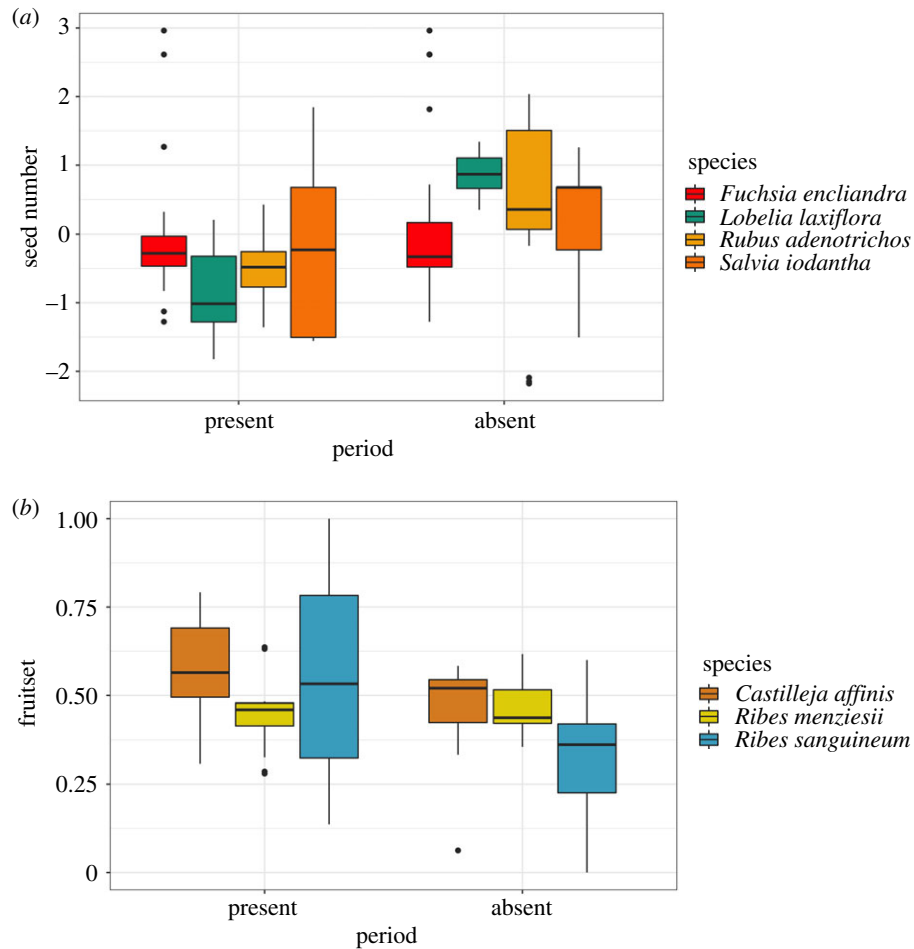
Figure 4. Boxplots showing the effect of period of sampling (migratory species present–absent) on (*a*) the scaled number of seeds per fruit in four Mexican plants and (*b*) fruit set in three California plants. (Online version in colour.)

its migratory journey. This difference has a consequence for the role the species occupies in the community, which becomes more important in the area in which it behaves as a specialist and apparently more efficient pollinator. This result has implications for trying to determine the resilience of natural communities to species loss. Early efforts at doing so assumed that species loss meant interactions loss, allowing no restructuring or rewiring of interactions (e.g. [30]). More recent efforts have tried to take into account the ability of natural systems to restructure through species role changes by allowing a certain level of interaction rewiring (e.g. [31]). Although we are still far from understanding what drives changes in species behaviours and what the consequences of these changes are, our study clearly shows that interaction rewiring may be common and is important for both sides of bipartite interactions like plant–pollinator networks. The existence of interaction rewiring might be more common in systems like ours adapted to annual migration processes, yet the frequency of this phenomenon across different ecosystems is not yet clear.

Global change impacts are particularly pressing in the case of migratory species, which are forced to shift their migratory behaviours in response to changes in the suitability of their breeding and wintering habitats [32]. Much global change research has been devoted to studying the changes to the migratory routes, departure or arrival dates [33] of migratory species, yet less attention has been given to the functional impacts that these changes could have within the natural communities that support them [34]. Indeed, migratory species transport nutrients and energy as well as other organisms (e.g. seeds, mollusks, parasites and pathogens, pollen grains) between distant locations [34],

thus coupling ecological communities throughout their migratory routes. Studies focusing on the interactions between migrant and resident species have shown that migrants can alter food web topologies, and the structure and dynamics of natural communities [34]. Migrants thus have the potential to affect ecosystem functioning across the different resident communities they connect in their journeys, and understanding their impacts requires of integrative studies linking biogeography to community ecology among other disciplines. In the case of hummingbirds in particular, migrant species are key players that increase plant–hummingbird network cohesiveness by interacting with a diverse set of plant species [35].

5. Conclusion

Recognizing the dynamic aspects of natural communities, as well as the potential for reorganization of their interaction networks, will increase our ability to predict responses to both natural and anthropogenic disturbances—including major drivers of biodiversity loss, such as land use and climate change. Climate change is expected to have significant impacts for biodiversity, including phenological shifts and latitudinal shifts in the distribution of many species as they track their climate niches, as well as changes to migration routes or even a cessation of migratory behaviours. As shown by our study, such changes in the distribution of migratory species of high conservation value with key roles in the communities could have indirect negative impacts on many other species, including plants and other pollinators, given the interdependencies of species within natural ecosystems.

8

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