From local adaptation to range sizes
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Synthesis
A main goal of this thesis was to find out how dispersal determines the colonization and establishment on new habitats, and how it ultimately explains variation in range sizes. It is already well known from previous studies that dispersal is a crucial step for the colonization of new habitats, and that the establishment in new locations is part of range expansion. Given that we already know this, why should we continue to study the effects of dispersal on range size expansion?

The answer in a nutshell: reaching a new distant patch does not necessarily ensure range expansion. Populations along the range borders likely experience very different conditions than populations that are in the center of the range. Thus, stasis in species range borders and a failure to expand their ranges can be caused by the lack of local adaptation to new conditions, either because of the absence of genetic variation, or because of too much gene flow that reverses local selection (Holt & Gomulkiewicz 1997). Understanding what happens with the populations along the species range borders and how dispersal affects those local populations will ultimately shed some light on range expansion and species range sizes (Holt & Keitt 2005). Providing evidence on the dual role of dispersal on local adaptation is the main aim of the first part of this thesis.

I showed using two independent experimental studies that dispersal exerts both negative and positive effects on colonization, extinction and local adaptation. My results are inspired by a simple scenario: from a mainland, individuals reached islands with very different conditions, i.e. these islands are composed of a different plant species, can vary in size and were initially empty or with only one competing species. Further immigration came only from maladapted individuals from the mainland. Under this scenario I found that dispersal exerts a positive effect on adaptation when dispersal rates were high (chapter 2). This is because even though most immigrants might not be well adapted to the new conditions, by chance some of them can bring the alleles to cope with these new conditions if genetic variation is high enough, thus spreading these advantageous alleles to the island population. However, too high levels of dispersal will exert a negative effect on adaptation (chapter 3). This is in line with several other studies suggesting that the relationship between dispersal and adaptation is bell-shaped (Garant et al. 2007, Fig. 1a). Although I did not find such a complete bell-shaped relationship in chapters 2 and 3, this is likely due to the different ranges of dispersal that were used in each study. In chapter 2 dispersal rates ranged from 0.5 to 2 mites/week, whereas in chapter 3 dispersal rates ranged from 2 to 10 mites/week. In chapter 2 the relationship between dis-
persal and adaptation was positive, whereas in chapter 3 the relationship between dispersal and adaptation was negative. In both experiments, local adaptation was highest around dispersal levels of 2 mites/week.

It is important to note that in other scenarios than those that I explored in this thesis, the relationship between dispersal and local adaptation might be different. While it is unknown in which way these relationships would differ, one could speculate Fig. 1b, c. For instance, if the local population is already adapted to the local habitat, irrespective of the exact rate, immigration might have a negative effect if immigrants come from a non-adapted population (via genetic load). Alternatively, if immigrant come from an already adapted population, then local adaptation is unnecessary, because immigrants are already adapted (Fig. 1c). Even though there are several possible scenarios, I believe that the scenario I studied in this thesis (Fig. 1a) is the most relevant for range expansion. For range expansion individuals need to reach areas outside their current range, and these novel areas will most likely be characterized by challenging conditions, to which they need to adapt.

Besides dispersal, there are many other factors that can affect colonization-extinction dynamics and adaptation, and thus affect range expansion. Firstly, because habitat that is ideal for a certain species is never homogeneously distributed (neither spatially nor temporary), the spatial configuration of the habitat (islands, reefs, patches of forest) can play an important role. Some of the first recognizing the importance of geographical features on biodiversity were MacArthur and Wilson. In their Island Biogeography Theory (IBT), they sketched how island size and isolation from a mainland (that can be translated in differences in dispersal) can drive biodiversity, adaptation and speciation via colonization-extinction dynamics. Although the effects of colonization and extinction on species richness were already demonstrated by many other theoretical, empirical and experimental studies, the role of evolution in island biogeography has never been experimentally tested before.
From IBT we know that dispersal should increase colonization success and that island size should affect extinction (MacArthur & Wilson 1967). Using experimental biogeography, I confirmed these predictions (chapter 2, see also Fig. 2 and 3). More importantly, I additionally examined how the same factors that influence extinction and colonization can affect local adaptation. In chapter 2 I found a positive effect of dispersal on local adaptation (Fig. 1a and in the green/blue area of Fig. 4) and a positive effect of island size on local adaptation (Fig. 4), thus confirming hypothesized, but previously undemonstrated predictions from IBT. However, my results from chapter 3 showed that this is not the complete picture, as even higher levels of dispersal (and thus even less isolated islands) reduce local adaptation (see left or yellow/green side of Fig. 4). Thus, IBT should incorporate this more complete picture of the relationship between island size, isolation (i.e. the inverse of dispersal) and local adaptation (Fig. 4). The reason why those scenarios (Fig. 2-4 yellow/green area) were not included in IBT is likely because being closer to the mainland, thus receiving an even higher influx of immigrants, might not change the relationship for colonization or extinction (Fig. 2 and 3). However, scenarios of less isolation (higher dispersal) do change the relationship with local adaptation and therefore have strong implications on the success of the population. For instance, small islands that are very close to the mainland have high colonization success and low extinction (Fig. 2 and 3). However, because of the high influx of immigrants the local population is composed of only non-adapted individuals (Fig. 4). These populations are therefore in a continuous state of maladaptation.

**Fig 2** Schematic representation of the effect of island size and dispersal from the mainland on colonization success. Colonization success decreases with isolation, but its effect is smaller when islands are large.
Fig 3  Schematic representation of the effect of island size and dispersal from the mainland on extinction risk. Smaller islands experience higher risk of extinction than large ones. Extinction risk is reduced when islands are less isolated from the mainland, as receiving more immigrants promotes demographic rescue.

Fig. 4 Schematic representation of the effect of island size and dispersal from the mainland on the level of local adaptation. Adaptation is positively affected by island size and attains a maximum at intermediate levels of dispersal (medium isolation).

Besides physical or abiotic factors, biotic factors can also affect the success of a population in colonizing and adapting to a new habitat, and consequently in expanding its range. For example, interspecific competition can reduce population size and increase extinction risk, because stochastic demographic fluctuations are likely to
affect smaller populations more than larger ones. In chapter 3 I showed that strong competition can lead to unsuccessful colonization, low population sizes and high extinction risk. These island populations do not have a chance to adapt to the local habitat, thus competition will therefore negatively impact range expansion. However, it is interesting that competition can be beneficial in some circumstances. When populations are receiving a large influx of immigrants, which otherwise will negatively impact adaptation (via genetic load), competition allows adaptation by purging the population of most of the maladapted immigrants. As the realized immigration is lower and selection is stronger, this allows for the benefits of dispersal on local adaptation. As I showed in chapter 3, those populations were as adapted as populations with lower dispersal levels but without the competitor. Some studies have shown that adaptation can be facilitated by interspecific competition, because it increases selection pressure and thus speeds up the adaptation process, or because it can promote resource partitioning and character displacement (Stuart et al. 2014, Osmond & Mazancourt 2013).

Outcomes of biological interactions can, nevertheless, be variable, as their effect can range from negative to positive. Furthermore, in the case of herbivores, there are interactions that are indirect as they are mediated by the host plants. For instance, the model species I used for the evolutionary experiment in chapters 2 and 3, Tetranychus urticae, is one of these cases. Herbivory by T. urticae is known to up-regulate tomato defenses, whereas herbivory by its competitor T. evansi can down-regulate tomato defenses (Sarmento et al. 2011, Godinho et al. 2015). Therefore, the effect of interspecific competition on adaptation might differ when using a different set of species from the ones I used in chapter 3.

In our experiment the island was already occupied with the competitor, so individuals of T. urticae needed to simultaneously adapt to the local habitat and to the competitor. Another scenario in which the competitor arrives after T. urticae may have had a different outcome, because adaptation to the local habitat can increase competitive abilities (Box 1). Therefore, interspecific competition might not have such a strong negative effect on adaptation.

**GIVEN BOTH POSITIVE AND NEGATIVE EFFECTS OF DISPERSAL, HOW DOES DISPERSAL ULTIMATELY AFFECT RANGE SIZE?**

With the first two experimental studies (chapters 2 and 3), I illustrated several mechanisms through which dispersal can affect range expansion. However, to understand how important these mechanisms are in the real world, observational studies jointly examining how dispersal and other factors drive species range sizes might provide a more complete picture. In chapter 4 I showed using theoretical models
that dispersal can play an important role in shaping species ranges by affecting the overall range size distribution within a dispersal guild and in chapter 5 I showed that range size positively correlates with traits associated with dispersal.

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Box 1. Adaptation to a challenging host increases competitive abilities

To successfully colonize new habitats, organisms need to cope with the selective pressure imposed by the local community. Differences in adaptation will help not only to cope with the exigencies of the new environment but also to avoid competitive exclusion. Here, I used a competition experiment to test whether females of two-spotted spider mite (Tetranychus urticae) with different levels of adaptation to a host plant (tomato) are better able to cope with competition from a phylogenetically related and tomato-adapted mite, the red mite (Tetranychus evansii).

**Competition experiment** - I used 3 different populations of T. urticae that differ on their level of adaptation to tomato. All populations are derived from the London strain, originally collected from the vineland region in Ontario, Canada (Grbić et al. 2011). The non-adapted population (N) is the original stock population adapted to bean plants (Phaseolus vulgaris variety “prelude”) on which it was reared for more than 6 years. From this original stock population, we created two lines with different adaptation levels to tomato: the medium adapted population (M) reared on tomato plants for the last 20 generations (see Alzate et al. 2017 - chapter 3) and the highly adapted population (H) reared on tomato plants for more than 100 generations. Females from all different treatments were sampled and placed on common garden for 2 generations before the competition treatment: iso-female lines were created by placing individual adult females on detached bean leaves on wet cotton for two generations to remove juvenile and maternal effects. After this procedure 3 females from each iso-female line were placed on a complete tomato plant either without interspecific competition or together with 3 females of T. evansi (competition treatment). Population sizes were recorded after 15 days.

**Results** - Population size in new colonized plants highly depends on the social context and adaptation to the environment (Fig.1a, Table 1). Populations that co-occur with T. evansi are significantly smaller than populations without the competitor (Fig. 1a). Populations that have never been exposed to tomato plants perform worse than the populations adapted to tomato plants, both without and with a competitor. The population of T. evansi is negatively affected by the presence of T. urticae. This effect increases with the adaptation of T. urticae to tomato, such that populations of T. evansi competing with the highly adapted populations of T. urticae have a significantly smaller population size than without a competitor (Fig. 1b, Table 1).
Fig. 1  Population size after one generation for a) *T. urticae* populations with different levels of adaptation to tomato plants with and without competition with *T. evansii*, and b) for *T. evansii* populations without and with competition with *T. urticae* with different levels of adaptation to tomato plants. Letters denote the three different adaptation levels of *T. urticae*: N – non-adapted, M – medium adapted, H – highly adapted.

Table 1  Summary of Generalized Linear Mixed model, with Poisson error distribution, testing the effect of adaptation on population size after one generation with and without competition between *T. urticae* and *T. evansii*. The presence of competition and the level of adaptation are considered fixed effects, and replicate and iso-female line are nested random effects.
Using a spatially explicit neutral model, I showed how neutral processes can drive different range size distributions depending on dispersal. In a scenario with strong dispersal limitation (a dispersal kernel with low mean dispersal distance), a large proportion of the species of the metacommunity attained small ranges and very few occupied the complete region. In contrast, in a scenario of low dispersal limitation, most of the species attained very large range sizes (chapter 4, Fig. 3). The positive effect of dispersal on range size is further confirmed by using a correlational study, which shows that range size is positively correlated with traits that are related to dispersal ability in reef fishes (chapter 5). Fishes that have pelagic eggs, high adult mobility and have large body size attain larger range sizes than fishes that have non-pelagic eggs, have low adult mobility and are smaller.

The positive relationship between dispersal and range size (shown in chapters 4 and 5) suggests that the negative effects of dispersal (shown in chapters 2 and 3) are outweighed by the positive effects, so that more dispersive species in general attain larger ranges. There are several possible explanations for why this is the case. Firstly, results from experiments in chapter 2 and 3 that show both positive and negative effects come from a particular scenario, where the new habitat that is colonized by immigrants is challenging for the individuals, so that migrating individuals often fail to establish a population. However, the situation for reef fishes might be different. The fish species I studied live on reefs (coral or rocky) within a single tropical region (TEP) and many of those species occupy only a small proportion of the available habitat. For these species, therefore, colonizing areas outside their species might not
bring a strong change of conditions, if those areas are still within the TEP. Examining what happens with populations that reach areas outside the tropical regions might show higher costs of dispersal.

Another possibility is that it is unnecessary to adapt to the local conditions to be able to attain larger ranges. Compared to mites, some reef fish species are highly dispersive (in terms of distance), so that dispersal can maintain populations as sinks far beyond their optimal habitats. As low dispersers will be less likely to do so, a positive relationship between dispersal and range size might arise, even if dispersing individuals fail to maintain stable, independent populations.

Another question is why within guilds of species with similar dispersal, variation in range sizes is so high (chapter 4). I hypothesize that differences in range sizes for low dispersive guilds might arise from differences in abundances (Box 2) or differences in species age or adaptation to the predominant conditions in the TEP. Species coming from temperate regions in general had smaller ranges than species coming from other tropical regions outside the TEP, despite their closer proximity. Possibly, this is because the latter are better adapted to the predominant climate in the TEP.

Although other studies have highly debated whether dispersal plays any role in explaining species range sizes, I have found strong, positive effects. In chapters 4 and 5 I numbered several reasons why previous studies have not been able to find a relationship between dispersal and range size in reef fishes. Firstly, one of the issues that researchers working on dispersal need to deal with is measuring dispersal. Because this is usually a difficult task, most of the studies have used proxies, i.e. traits that correlate with dispersal (e.g. body size, pelagic larval duration, type of egg). Secondly, usually correlational studies have used only a subset of the species of interest, as they were constrained by the availability of data on the trait of interest (pelagic larval duration in the case of reef fishes). In chapter 5, I showed that, for the particular case of reef fishes in the TEP, using a subset of species leads to very different result regarding the relationship between dispersal and range size than using the complete species pool. This was due to the non-randomness of the species set for which the trait of interest has been measured. Therefore, to reach correct conclusions it is not only important to study a large number of species, but also that these species are a random sample from the regional species pool.

Additionally, the spatial configuration of suitable habitat can have a strong effect on how dispersal might affect range expansion (suggested by experiments in chapter 2) and may thus likely affect the range size - dispersal relationship. In chapter 4 I showed that in a simple scenario (a continuous homogenous habitat, no evolution and neutral ecological processes), dispersal should have a positive effect on range size. I also showed in chapter 5 using statistical models that several traits related to dispersal (body size, spawning mode, adult mobility) correlated positively
with range size of reef fishes in the Tropical Eastern Pacific (TEP). It is important to note that the TEP represents the simplest marine geographical scenario: a relatively continuous habitat with clear limits. It is possible that in other scenarios of habitat configuration, like the scattered habitats typical from other tropical regions, outcomes might differ from the ones in the TEP. Thus, it is possible that we can see a positive effect of dispersal on range sizes not only because I used a complete data set of species (which I showed important to reach these conclusions), but also because of the particular habitat configuration of the TEP, which merits further study.

FUTURE DIRECTIONS

The relationship between dispersal and local adaptation

The dispersal-adaptation relationship suggested by chapter 2 and 3 might be only applicable when both the local population and the immigrants are not adapted to the new local habitat. I previously suggested that other relationships might be expected when the local or the immigrants are adapted (Fig. 1). These predictions can be tested using the same study system that I used in chapters 2 and 3 (experimental evolution using the two-spotted spider mite).

The relationship between dispersal and range size when both the local population and the immigrants are not adapted to the local conditions (Fig. 1a) might, as I suggested before, be the most relevant situation to understand how populations become locally adapted. Along the species range borders habitat might be considerably different than in the center of their range, thus when immigrants from the center of the distribution arrive to the border or further, they might encounter new habitats towards which they are not adapted. Depending on how well they perform in these new habitats, this might result in range expansion. I found that dispersal can have positive and negative effects on adaptation when locals and immigrants are not adapted to the local conditions (chapter 2 and 3), which suggests, given the dispersal rates used in each study, that the real relationship between dispersal and adaptation is bell-shaped (Fig. 1a). Ideally, such a bell-shaped relationship should be demonstrated within a single study. A new experiment using a wider range of dispersal (e.g. from 0.5 or less mites/week to 10 or more mites/week) than I used before might be most suitable for reaching this objective.

The relationship between dispersal of non-adapted immigrants and local adaptation when the local population was already adapted is expected to be negative, due to genetic load (Fig. 1b). This situation might be relevant to understand range shrinkage in some particular scenarios. For example, secondary contact between two populations adapted to contrasting habitats might cause the flow of maladapted
genes in both directions. This can wipe out local populations vulnerable to extinction, thus leading to range shrinkage. These predictions could be tested by using the adapted line of *T. urticae* as the first population on the islands, which are then receiving non-adapted immigrants from the mainland.

A third possible scenario is that both the local population and the population mainland experience similar environmental conditions, and that both populations are therefore highly adapted to both the mainland and island conditions. In this case, no relationship between dispersal and local adaptation is expected (Fig. 1c). Only in the case that either the island or mainland population is so small that there is the risk of in-breeding, dispersal can increase genetic variation and thus maintain local adaptation.

**The relationship between dispersal and range size**

The utility of using spatially explicit models to understand macroecological patterns, for which my study in chapter 4 is a first attempt, does not only need to be restricted to range size distribution patterns, as it may also be possible to explain several other macroecological patterns. For instance, the relationship between species abundance and range size, the relationship between species age and range size, and the relationship between range size and latitude might all be explained with my spatially explicit neutral model. For instance, I have already explored the relationship between abundance and range size (Box 2). Interestingly, I found that this relationship is not straightforward: its strength can be mediated by dispersal and by sampling intensity (Box 2). Thus, a strong positive relationship will be found in low dispersive guilds, while the relationship is expected to be less strongly positive for highly dispersive guilds. It is easy to understand why this might be the case. For a highly dispersive guild, to attain larger ranges it needs a minimum of only two highly dispersive individuals (in a very extreme and hypothetical case). However, a low dispersive guild can only attain larger ranges in very small steps, as dispersing individuals will never be able to highly expand the range. The synthesis and analysis of multiple, existing datasets on abundances and range sizes of various guilds, differing in average dispersal levels, is needed to empirically test whether these predictions hold.

I previously discussed the importance of habitat configuration on mechanisms for range expansion (results from chapter 2), and consequently range sizes (suggested in chapter 4 and 5). This raises the question whether a relative continuous habitat is a prerequisite for the positive range size - dispersal relationship that I observed for reef fishes in the TEP (chapter 4 and 5), or whether such positive relationships are also possible in regions with other habitat configurations, such as the Caribbean. There are several, complementary, approaches to tackle this question. Firstly, it is possible to use a modelling approach to compare how range size distributions will differ between a continuous and a discontinuous habitat. Another sim-
ple way to examine how range expansion will be affected by the underlying habitat configuration is by running the same model, but with only a single species, under different scenarios of habitat configuration and using different dispersal kernels and including connectivity due to e.g. ocean currents. I expect that a very low disperser will be more affected by isolation than high dispersers and that range expansion will be easier in more continuous habitat than in fragmented habitat. Finally, it is possible to use empirical data to investigate the role of habitat configuration in driving range sizes. For instance, one could examine the range size-dispersal relationships of different regions with different habitat configurations, e.g. the Tropical Eastern Pacific vs. the Greater Caribbean.

**Box 2. The relationship between abundance and range size**

Besides studying the relationship between range size and dispersal, the spatially explicit neutral model used in chapter 4 also allows us to explore another not completely understood pattern: the relationship between range size and abundance. Here, I explored what relationship between range size and abundance is expected in a neutral context. I tested whether a positive abundance-range size relationship is the result of a sampling artefact when quantifying (local) abundance (hypothesized by Gaston et al. 1997). Furthermore, I explored how this relationship is modulated by the dispersal abilities of the species, something that has not been yet investigated.

**Methods** - I explored how variation in dispersal and different sampling efforts affects the range size-abundance relationship. I ran 100 simulations using two extreme scenarios of dispersal ($X_{\text{mean}} = [0.02, 0.4]$). I plotted the relationship between range size and abundance (all simulations combined) for four different sampling scenarios: 1) sampling 100% of the individuals (‘exhaustive sampling’), 2) randomly sampling 1% of the individuals (‘random sampling’), 3) exhaustive sampling within a single location harboring 1% of all the individuals in the lattice (‘extremely clustered sampling’) and 4) exhaustive sampling within ten random locations, each harboring 1% (thus summing up to 10%) of all individuals in the lattice (‘moderately clustered sampling’).

**Results** - The observed range size abundance relationship depends largely on dispersal, but also on the way abundance is measured, and on the sampling effort (Fig. 1). Under the exhaustive sampling scenario, a positive relationship between abundance and range size is clear at low, but not at high levels of dispersal (Fig.
For low dispersal guilds, the positive abundance-range size relationship is maintained even under a scenario of incomplete, random sampling (Fig. 1a, b). However, when sampling effort is more clustered, the observed relationship strongly deviates from the real relationship (Fig. 1c, d). For high dispersal guilds, the pattern when using total abundance is more logarithmic. Thus, for very low dispersal, range sizes are small, but with a small increase in abundance range size rapidly increases. This increase becomes less strong when randomly sampling 1% of the total number of individuals (Fig. 1f), but when sampling is clustered in one or 10 localities, all observed species tend to attain larger ranges (as species with smaller ranges are not observed), irrespective of their abundance (Fig. 1g, h).

**Discussion** - Besides explaining range size distributions, the spatially explicit null model used in chapter 4 can also help explaining positive relationships between species’ abundances and range size. While such patterns have ample empirical support (Gaston 2003), it is still unclear what mechanism (or mechanisms), of the several that have been proposed, is responsible for them (Gaston *et al*. 1997, Gaston 2003).

The neutral model allowed for testing the roles of sampling intensity and dispersal ability in driving observed abundance-range size relationships. I showed that, contrary to some other hypotheses (Gaston *et al*. 1997), positive relationships between range size and abundance are expected (as long as dispersal rates are sufficiently low) and are possible to observe when organisms are exhaustive sampled. However, such relationships are not observed when abundance estimates are based on incomplete samples that are clustered in space.

In practice, exhaustively sampling 100% of the individuals is impossible and sampling intensity is often clustered in space (with a few sites with high sampling intensity and remaining areas hardly sampled), which is a possible explanation why empirical studies do not always show positive range size-abundance relationships. In addition, our neutral model also pointed at the importance of dispersal for relationships between abundance and range size. Within guilds with species with relatively high dispersal, relationships between range size and abundance are more logarithmic, meaning that species with very few individuals attain small ranges (e.g. singletons), but the abundance needed to be able to reach maximum range is much lower than for low dispersers. In other words, for a highly dispersive species to attain a large range it is sufficient to have only 2 highly dispersive individuals. However, for a low dispersive species to attain large ranges it would necessary increase in number of individuals that can reach further places in small steps.
Fig. 1 Effect of dispersal (low vs high) and sampling intensity on the range size-abundance relationship. The effect of dispersal was explored for two contrasting dispersal kernels that differed on the mean dispersal distance: a-d) low dispersal – $X_{\text{mean}} = 0.02$, and e-h) high dispersal – $X_{\text{mean}} = 0.4$. The effect of dispersal was explored by examining four different sampling scenarios: a, e) exhaustive sampling - sampling 100% of the individuals, b, f) random sampling - 1% of the individuals are randomly sampled, c, g) extremely clustered sampling - exhaustive sampling within a single location containing 1% of all the individuals in the lattice, and d, h) moderately clustered sampling - exhaustive sampling within ten random locations, each harboring 1% (thus summing up to 10%) of all individuals in the lattice. Range size is expressed as a proportion of the total lattice size. Differences in color intensity represent differences in the number of data points in each position. Measurements of abundance are given in absolute numbers for panels a-c and e-g, whereas the average of abundances for 10 random locations was used for panels d and h.
CONCLUDING REMARKS

What have we learned about the role of dispersal for range size?
In this thesis, I investigated the role of dispersal in driving local adaptation to new habitats and ultimately, range sizes. Although it is clear that dispersal is a key characteristic of organisms in explaining their ability to reach new habitats, to locally adapt and to obtain large range sizes, there is still a lot that we do not understand. For example, within species with similar dispersal abilities, a large range of range sizes is possible. Understanding local adaptation and range sizes is not only of fundamental interest, but also of high applied value. Range size is one of the strongest predictors of extinction rates, so explaining what drives range sizes will also help explaining what drives species’ vulnerability to extinctions. Furthermore, ongoing global changes such as habitat loss and climate change will likely not only affect the need, but also the ability of species to adapt to novel environments. Therefore, I consider improving our understanding in what drives the ability of species to adapt and maintain large ranges as one of the greatest scientific challenges, and I would be happy to continue contributing to resolving this challenge.