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RESEARCH PAPER

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# Experimental island biogeography demonstrates the importance of island size and dispersal for the adaptation to novel habitats

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## Abstract

**Aim**: Island biogeography theory describes how island size and isolation determine population colonization success. Large islands sustain larger populations than small ones and experience less demographic stochasticity, thus a lower extinction risk. Nearby islands are more likely to be colonized than distant ones, because they receive more immigrants from the mainland. However, local conditions on islands are often different from those on the mainland; therefore, populations on recently colonized islands also need to adapt. Island size and isolation are known to impact the build-up of genetic variation necessary for adaptation; hence, we integrated island biogeography with evolution experimentally to gain a better understanding of the roles of island size and isolation in biodiversity patterns.

**Location**: Laboratory, Ghent University, Belgium.

**Time period**: October 2013 to June 2014.

**Major taxa studied**: Two-spotted spider mite (*Tetranychus urticae*).

**Methods**: Using experimental evolution, we studied the effects of island size and isolation on colonization, extinction and adaptation of the two-spotted spider mite to new islands. The mainland population consisted of bean plants and the islands of tomato plants (a known challenging condition). Islands differed in their size (number of plants) and in the number of immigrants (females, the dispersive stage) they received from the mainland.

**Results**: Island size and dispersal decreased extinction risk and increased colonization success and adaptation. Populations on small islands, which are most affected by extinction, were rescued demographically by an increase in dispersal. However, they were never able to adapt.

**Main conclusions**: Evolutionary rescue via dispersal is possible only when populations are sufficiently large; small populations cannot adapt, because they lack the genetic variation necessary for local adaptation. Hence, in addition to the effects of island size and dispersal on the ecological processes of colonization and extinction, our results show that island size and dispersal can jointly affect the evolutionary process of adaptation to novel habitats.

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KEYWORDS
dispersal, experimental evolution, island biogeography, island size, local adaptation, spider mites

## 1 | INTRODUCTION

Since the late 1960s, when MacArthur and Wilson released their island biogeography theory (IBT), ecologists and evolutionary biologists have become familiar with the idea that the number of species on islands depends on their size and their distance from the mainland, which affect rates of extinction and colonization. Smaller habitats (or analogously, habitats of lower quality or that are more disturbed) offer fewer resources to maintain an adequate population size and are therefore more vulnerable to extinction (Fahrig, 1997; MacArthur & Wilson, 1967). More isolated habitats have the additional disadvantage of being more difficult to colonize because they receive fewer immigrants, hence they are deprived of a possible demographic rescue effect (Brown & Kondric-Brown, 1977; MacArthur & Wilson, 1967). The nature of the relationship between extinction and isolation/dispersal has been included as one of the 50 fundamental questions 50 years after the first appearance of IBT (Patiño et al., 2017).

It is generally accepted that in order to colonize new islands successfully, immigrants need to adapt to the local conditions, because islands often experience different environmental characteristics from the mainland. Although its potential importance has been acknowledged in the seminal monograph by MacArthur and Wilson (1967), this process has not been incorporated into the IBT. A reduction of island size and an increase in isolation (hence a reduction of immigration rates) not only affects population extinction and colonization but can also, via the loss or absence of demographic and evolutionary rescue, impact the capacity of populations to adapt to new habitats (Alzate, Bisschop, Etienne, & Bonte, 2017; Blanquart, Gandon, & Nuismer, 2012; Bolnick & Nosil, 2007; Ching et al., 2012; Cuevas, Moya, & Elena, 2003; Garant, Forde, & Hendry, 2007; Hufbauer et al., 2015; Lachapelle, Reid, & Colegrave, 2015). Demographic rescue buffers populations against stochastic fluctuation in population sizes and may additionally facilitate adaptation to new conditions by extending population age and thus the time needed to adapt. Evolutionary rescue is a direct consequence of the integration of new genes and a reduction of inbreeding.

Several studies have provided important insights into the independent roles of dispersal (Alzate et al., 2017; Bolnick & Nosil, 2007; Ching et al., 2012; Cuevas et al., 2003) and population size (Lachapelle et al., 2015) on adaptation. Evolutionary outcomes of adaptation are more robust and repeatable in larger populations than in small ones, which has been suggested to be attributable to the stronger effect of history and stochasticity on small populations (Lachapelle et al., 2015). High rates of dispersal have often been shown to have a negative effect on the adaptation process by imposing genetic load (Alzate et al., 2017; Bolnick & Nosil, 2007; Cuevas et al., 2003; but see Ching et al., 2012), particularly when dispersal is random (Jacob et al., 2017). In order to understand fully how island size and dispersal act together to affect colonization and extinction, we need to understand how island size and dispersal jointly drive the ability of new island populations to adapt locally, and thus thrive, in their new environment. Integrating biogeography with experiments is a promising next step to a more comprehensive eco-evolutionary island biogeography. Although experimental island biogeography has already been performed using natural and experimental islands examining plants, arthropods and protozoans (see Have, 1987; Schoener, 1988; Wilson, 2010), this has been from a purely ecological perspective, related to species colonization, immigration and extinction. However, there have been no attempts experimentally to test the role of evolution in island biogeography.

An ideal species with which to test the joint roles of dispersal and island size experimentally in the context of island biogeography is the two-spotted spider mite (*Tetranychus urticae*). This is a generalist herbivore with short generation times, and small enough for long-term and replicable experiments. It has been a model organism in which to study adaptation (Agrawal, 2000; Alzate et al., 2017; Bonte et al., 2010; Egas & Sabelis, 2001; Fry, 1990; Gould, 1979; Kant, Sabelis, Haring, & Schuurink, 2008; Magalhães, Fayard, Janssen, & Olivieri, 2007), the evolution of dispersal (Bitume et al., 2011, 2014) and range expansion (van Petegem et al., 2016, 2018). Here, we simulated a mainland–island system experimentally, in which the mainland is composed of bean plants and the island of tomato plants, to test for the effect of island size and dispersal (isolation) on adaptation of the two-spotted spider mite to a new host plant. Islands varied in size (number of plants) and in the number of immigrants received from the mainland (ancestral population on the ancestral host plant). We followed the adaptation process to the new host plants during 20 generations and tested for differences in adaptation to tomato between treatments (after removing putative epigenetic effects) at two time points using a fitness proxy.

## 2 | METHODS

### 2.1 | Study species

The two-spotted spider mite *Tetranychus urticae* Koch, 1836 (Acari: Tetranychidae) is a cosmopolitan generalist herbivore that feeds on a variety of plant species and families (Bolland, Gutierrez, & Flechtmann, 1998; Gotoh, Bruin, Sabelis, & Menken, 1993). *Tetranychus urticae* attains a small body size (female size *ca*. 0.4 mm in length), has a high fecundity (1–12 eggs/day) and a short generation time (11–28 days), which makes it an ideal model for experimental evolution studies (Agrawal, 2000; Alzate et al., 2017; Bonte et al., 2010; Egas & Sabelis, 2001; Fry, 1990; Gould, 1979; Kant et al.,

2008; Magalhães et al., 2007). Previous studies have observed a response to selection after five generations (Agrawal, 2000) and adaptation after 15–20 generations of selection to a new host (Alzate et al., 2017; Magalhães, Blanchet, Egas, & Olivieri, 2009). Long-distance dispersal occurs by wind, because they do not produce silk to disperse as in other species from the same genus (Boyle, 1957); hence immigration rates are directly distance dependent, as immigration success declines exponentially with distance when island size is kept equal. Long-distance dispersal allows *T. urticae* to move from a desiccated host onto a more succulent one (Bancroft & Margolies, 1999).

## 2.2 | Experimental evolution

We used a mesocosm experiment to test the effects of dispersal and island size on the adaptation of *T. urticae* to a new host plant. The mainland population (London strain), which was originally collected from the vineland region in Ontario, Canada (Grbić et al., 2011), is adapted to bean plants (*Phaseolus vulgaris* variety 'prelude'), on which it has been reared for > 200 generations.

The experimental populations were initiated on islands composed of 3-week-old tomato plants (*Solanum lycopersicum* variety 'money maker'). All populations started with three individual adult females from the mainland population. The islands varied in the number of plants (island size) and the number of immigrants they received (bi)weekly from the mainland population (dispersal level). We used three island sizes (islands composed of one, two or four tomato plants) and three dispersal levels (.5, 1 and 2 adult female mites/week) (Supporting Information Figure S1). Each dispersal–island size treatment combination was replicated five times. Plants within each island were put close together with a cord ring to allow dispersal between them. The islands were placed on yellow sticky traps (Pherobank) to avoid dispersal between them. The islands (tomato plants with mite populations) were kept in a climate-controlled room at 25 ± .5 °C with a 16–8 h light–dark regime. All islands were refreshed every 2 weeks by transferring all leaves and stems with mites from the old to the new island. The experiment was performed for 20 generations, over a 7-month period.

To examine the effect of dispersal and island size on population size and extinction, we counted the number of adult females (a proxy of population size) present on each experimental island at two different time points (generations 11 and 16) and recorded the number of extinction events during 16 generations. Populations were generally 10–15 times larger than the numbers we present here when we also include juveniles and males (S2 in De Roissart, Wang, & Bonte, 2015). Using the information on extinction events, we calculated the life span of the populations on islands. Several population life spans can be recorded per island if, on a single island, there are several extinction and colonization events. Given that population size and adaptation might increase with the age of the population, we estimated population age for the last population present on the tomato islands as the number of generations after the last colonization event. Colonization time was calculated as the number of days for which the island was unoccupied between an extinction and colonization event. Given that several colonization times can be reported per island, we used the last colonization time as they might not be independent from each other. For a graphical representation of colonization and extinction events, life spans and colonization time, see Supporting Information Figure S2.

To assess the influence of dispersal and island size on adaptation, we performed fitness experiments at generations 11 and 20. Each time, we took samples (one to five adult females depending on mite population sizes on plants) from each island to start iso-female lines. Individual females were reared separately on a common garden (four bean leaf discs, 5 cm in diameter, on cotton wool soaked in distilled water) for two generations to remove juvenile and maternal effects (Kawecki et al., 2012; Magalhães, Blanchet, Egas, & Olivieri, 2011). After these two generations on common garden, two teleiochrysalises (last quiescent stage before adulthood) were used for testing the level of adaptation of every iso-female line using fecundity as a proxy for fitness, on tomato leaf discs (two discs, 3 cm in diameter). We recorded total fecundity (number of eggs) after 6 days from daily photographs. Eggs usually start hatching after 5–6 days, thus making it difficult to estimate fecundity after that time. As a control, we also performed a fitness test for females coming from the mainland at generation 11 and 20 in the same manner as with the females coming from the experimental islands.

## 2.3 | Data analysis

### 2.3.1 | Effect of dispersal and island size on colonization, population life span, abundance and extinction (before common garden)

To test the effects of dispersal and island size on colonization time, we used generalized linear models with Poisson error distribution. The full model contained dispersal, colonization and its interaction effect as fixed factors.

To test the effects of dispersal and island size on population life span, we used a survival analysis, with a Cox proportional hazard mixed effects model. The full model included dispersal, island size and their interaction as fixed effects and island as a random effect (given that each island population can undergo several extinction–colonization events, several life spans are counted). Population life spans that were truncated because of the end of the experiment were considered as censored data. Our final model was tested to meet the proportional hazard assumption.

We examined the effect of island size and dispersal on population size on the tomato islands (before removal of maternal effects) after 11 and 16 generations using linear models. The model to explain population size also included population age (number of generations after successful colonization) as a fixed factor, because older populations are expected to be larger than younger ones. Population size was logarithmically transformed to meet the normality assumption of residuals.

For testing the effect of island size and dispersal on the number of extinction events, we used generalized linear models with a Poisson error distribution. Both island size and dispersal were considered as fixed factors. Our final model contained island size and dispersal (but not their interaction).

### 2.3.2 | Effect of dispersal and island size on female fecundity (after common garden)

The effect of dispersal and island size on adaptation was tested using linear mixed models, with a Gaussian error distribution. The full model included three fixed factors [generation (two levels: generation 11 and 20), dispersal (three levels) and island size (three levels)] and two random factors [replicate (islands) and population age]. Fecundity was standardized by subtracting the mean fecundity of the female mites from the mainland population from the fecundity of each individual from the experimental islands. Separate analyses for generations 11 and 20 were performed using linear mixed models, also with a Gaussian error distribution. Dispersal and island size were included as factorial fixed effects, and replicate (island) and population age were included as random effects. A post hoc test was performed to test for differences between the least squares means of treatments using the function *difflsmeans* from the package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2016). Degrees of freedom were calculated with Satterthwaite's approximation.

Model selection for all statistical models was carried out by removing non-significant effects in a stepwise manner (based on log-likelihood ratio tests) until only significant effects remained. Analyses were performed in R version 3.3.1 and the R packages lme4 (Bates, Mächler, Bolker, & Walker, 2015), lmerTest (Kuznetsova et al., 2016), MuMIn (Barton, 2016) and coxme (Therneau, 2015).

## 3 | RESULTS

### 3.1 | Effect of dispersal and island size on colonization time, population life span, abundance and extinction

Both island size and dispersal affected population colonization time ($\chi^2$ = 146.8, d.f. = 1, $p$ < .0001). Colonization time decreased significantly with island size (estimate= −1.99, *SE* = .34, $z$ = −5.9, $p$ < .0001) and dispersal (estimate = −2.44, *SE* = .42, $z$ = −5.8, $p$ < .0001; Figure 1). When immigration was low, large islands were colonized earlier than small ones. However, when immigration was high, all islands, irrespective of their size, were colonized fast.

Both island size and dispersal affected population life span (Figure 2; $\chi^2$ = 53.17, d.f. = 3.7, $p$ < .0001). Populations had a longer life span on larger islands [hazard ratio (HR) = .69, $z$ = −3.79, *SE* = .09, $p$ < .0001)] and on islands receiving more immigrants (HR = .24, $z$ = −4.96, *SE* = .28, $p$ < .0001). Eighty per cent of populations on small islands with low dispersal attained life spans of a maximum of two generations, whereas all populations on large islands with the highest level of dispersal had the maximum achievable life span in our experiment (16 generations).

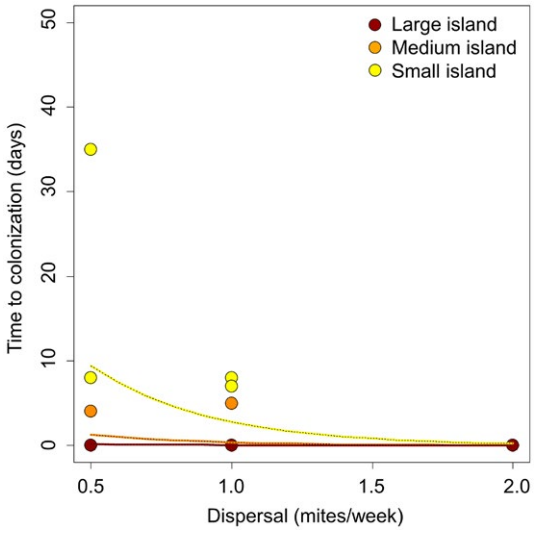


**FIGURE 1** Island colonization time decreases with island size and dispersal. The fitted lines were estimated from the generalized linear model with Poisson error distribution

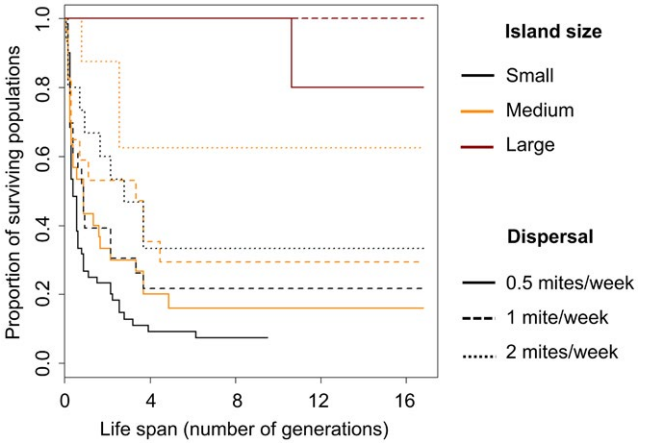


**FIGURE 2** Life span of population on island is positively affected by island size and dispersal

Island size had a positive effect on population sizes (number of adult females) on the experimental plants after both 11 and 16 generations ($\chi^2$ = 27.04, d.f. = −1, $p$ = .0001 and $\chi^2$ = 29.2, d.f. = −1, $p$ < .0001, for generations 11 and 16, respectively; Figure 3). Larger islands reached on average higher population sizes than smaller islands (79 vs. 25 females after 11 generations, estimate = .38, *SE* = .09, $t$ = 4.15, $p$ = .0001; and 73 vs. 15 females after 16 generations, estimate = .54, *SE* = .05, $t$ = 9.72, $p$ < .0001). Population age had a positive effect on population size only after 11 generations (estimate = .13, *SE* = .03, $t$ = 3.73, $p$ = .0005).

Both island size and dispersal affected the probability of population extinction (Figure 4; $\chi^2$ = 42.93, d.f. = 1, $p$ < .0001). Populations

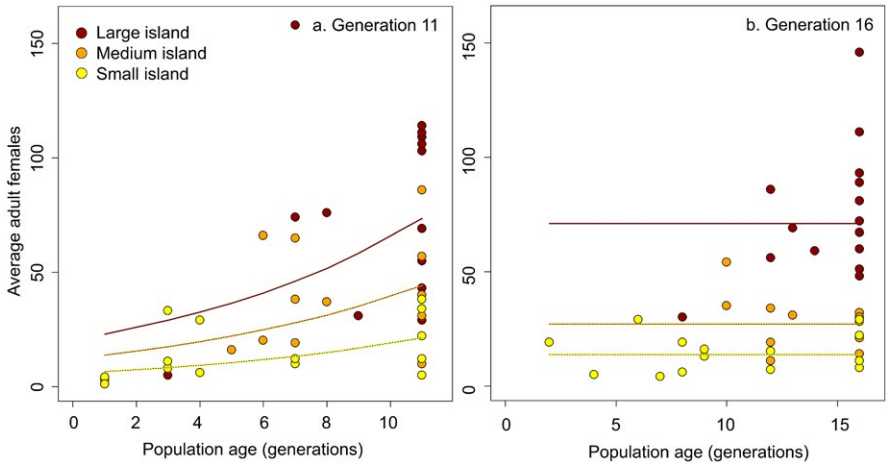


**FIGURE 3** Effect of population age and island size on population size after 11 (a) and 16 (b) generations of the evolutionary experiment

on small islands experienced on average significantly more extinction events than populations from large islands (8.7 vs. 2.4 extinctions; estimate = −.43, *SE* = .14, *z* = −3.14, *p* = .002). An increase in dispersal significantly reduced the extinction probability from on average 5.56 extinctions with low dispersal to .40 extinctions with high dispersal during the time the experiment lasted (estimate = −1.76, *SE* = .38, *z* = −4.63, *p* < .0001).

### 3.2 | Effect of island size and dispersal on adaptation to tomato

Adaptation to tomato islands increased from generation 11 to 20 (estimate = .96, *SE* = .30, *t* = 3.21, *p* = .002; Table 1; Figure 5). In addition, there was a significant interaction between generation and island size and between generation and dispersal (Table 1).

After 11 generations of adaptation to tomato, the effect of dispersal on female fecundity was positive only for populations on small islands (Figure 5; Table 1). Additionally, only at low dispersal levels (.5 mites/week) did island size have a positive effect on fecundity. However, mean female fecundity for all islands populations was within the same standard deviation range as that of females from the mainland (Figure 5).

After 20 generations, fecundity increased with an increase in dispersal and island size (Figure 5; Table 1). Female fecundity was lowest in populations from small islands, although the effect of dispersal was difficult to assess owing to the large variance on small islands. Female fecundity was highest in populations with the highest level of dispersal on medium-sized and large islands, and in populations with the second highest dispersal level on large islands. Female fecundity for these populations was higher than the fecundity of females from the mainland (Figure 5).

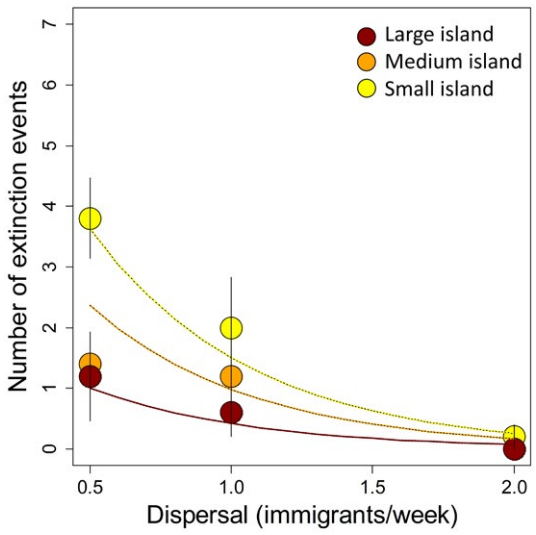


**FIGURE 4** The number of extinction events decreases with an increase of dispersal and island size

## 4 | DISCUSSION

In the present study, we showed how experimental evolution can shed light on the evolutionary aspects of IBT, because it allows chance/drift to be separated from determinism. Although IBT has mostly been restricted to understanding patterns of species richness on islands as a result of colonization–extinction processes (affected by dispersal from the mainland and island size), MacArthur and Wilson (1967) did mention a few evolutionary considerations about adaptive changes after colonization: 'Evolution on islands and archipelagos can eventually lead to the formation of new, autochthonous species. In order for evolution to proceed to this degree, islands must be relatively large and stable, otherwise populations will not survive long enough to undergo sufficient local adaptation' (p. 180). In other words, island size should have a positive effect on population survival and, eventually, adaptation. In spite of the importance of adaptation for successful colonization, adaptive radiation and speciation,

**TABLE 1** The effect of island size and dispersal on adaptation

| | Effect | Estimate | *SE* | *t* | *p* |
|---|---|---|---|---|---|
| All generations combined | Intercept | −6.40 | 4.98 | −1.28 | .202 |
| | Medium island | −3.84 | 6.13 | −.63 | .533 |
| | Small island | 8.36 | 8.46 | .99 | .325 |
| | 1 mite/week | .21 | 6.80 | .03 | .976 |
| | 2 mites/week | −7.68 | 6.85 | −1.12 | .265 |
| | **Generation 20** | **.96** | **.30** | **3.21** | **.002** |
| | Medium island * 1 mite/week | −2.75 | 4.13 | −.67 | .513 |
| | Small island * 1 mite/week | 10.10 | 5.63 | 1.79 | .080 |
| | Medium island * 2 mites/week | .59 | 4.23 | .14 | .891 |
| | Small island * 2 mites/week | 3.06 | 5.99 | .51 | .611 |
| | Medium island * Generation 20 | .06 | .37 | .16 | .874 |
| | **Small island * Generation 20** | **−1.31** | **.53** | **−2.47** | **.015** |
| | Generation 20 * 1 mite/week | .25 | .40 | .63 | .530 |
| | **Generation 20 * 2 mites/week** | **.97** | **.42** | **2.30** | **.023** |
| Generation 11 | Intercept | 5.25 | 2.11 | 6.76 | .015 |
| | Medium island | −5.25 | 3.22 | −1.63 | .108 |
| | **Small island** | **−8.50** | **4.22** | **−2.02** | **.048** |
| | 1 mite/week | .50 | 3.33 | .15 | .881 |
| | 2 mites/week | 1.42 | 3.22 | .44 | .661 |
| | Medium island * 1 mite/week | 1.50 | 4.51 | .33 | .741 |
| | Small island * 1 mite/week | 11.42 | 6.50 | 1.76 | .083 |
| | Medium island * 2 mites/week | 2.92 | 4.55 | .64 | .524 |
| | Small island * 2 mites/week | 10.50 | 6.44 | 1.63 | .108 |
| Generation 20 | Intercept | 11.8 | 2.33 | 6.11 | <.0001 |
| | Medium island | −.23 | 4.42 | −.05 | .958 |
| | **Small island** | **−14.23** | **6.38** | **−2.23** | **.032** |
| | 1 mite/week | 7.32 | 3.64 | 2.01 | .052 |
| | **2 mites/week** | **13.77** | **4.42** | **3.11** | **.003** |
| | Medium island * 1 mite/week | −10.32 | 6.71 | −1.54 | .132 |
| | Small island * 1 mite/week | 8.18 | 9.15 | .89 | .378 |
| | Medium island * 2 mites/week | −.52 | 7.16 | −.07 | .943 |
| | Small island * 2 mites/week | −13.77 | 11.2 | −1.23 | .227 |

*Note*. We ran the following three statistical models. (a) To test whether adaptation to tomato increases with time, we ran a linear mixed model with Gaussian error distribution for the effect of island size, dispersal and generation on fecundity. The full model included three fixed factors [island size (one, two or four tomato plants), dispersal (.5, 1 and 2 mites/week) and generation (11 and 20)] and two random factors [replicate (five islands per treatment combination) and population age]. (b) We ran a linear mixed model with Gaussian error distribution for the effect of island size and dispersal on adaptation for generation 11. The full model included two fixed factors (island size and dispersal) and two random factors (replicate and population age). (c) We ran a linear mixed model with Gaussian error distribution for the effect of island size and dispersal on adaptation for generation 20. The full model included two fixed factors (island size and dispersal) and two random factors (replicate and population age). Bold values indicate significant effects at the level of .05.

the joint effects of island size and dispersal on adaptive changes after colonization have not been explored in detail previously.

Our results confirm the theoretically expected negative effects of isolation and positive effects of island size on population colonization and extinction. Extinction events were much higher on small islands than on large ones, which is likely to be attributable to the smaller population sizes that small islands can sustain; populations of the same age (16 generations) were 4.6 times smaller on small islands than on large ones. In addition, we showed that dispersal can help populations by reducing their extinction rates, which is especially important for populations on small islands. These populations have on average four extinction events when dispersal is low and almost zero extinction events when dispersal is high. Dispersal thus reduces the chances of extinction by providing a rescue effect. This

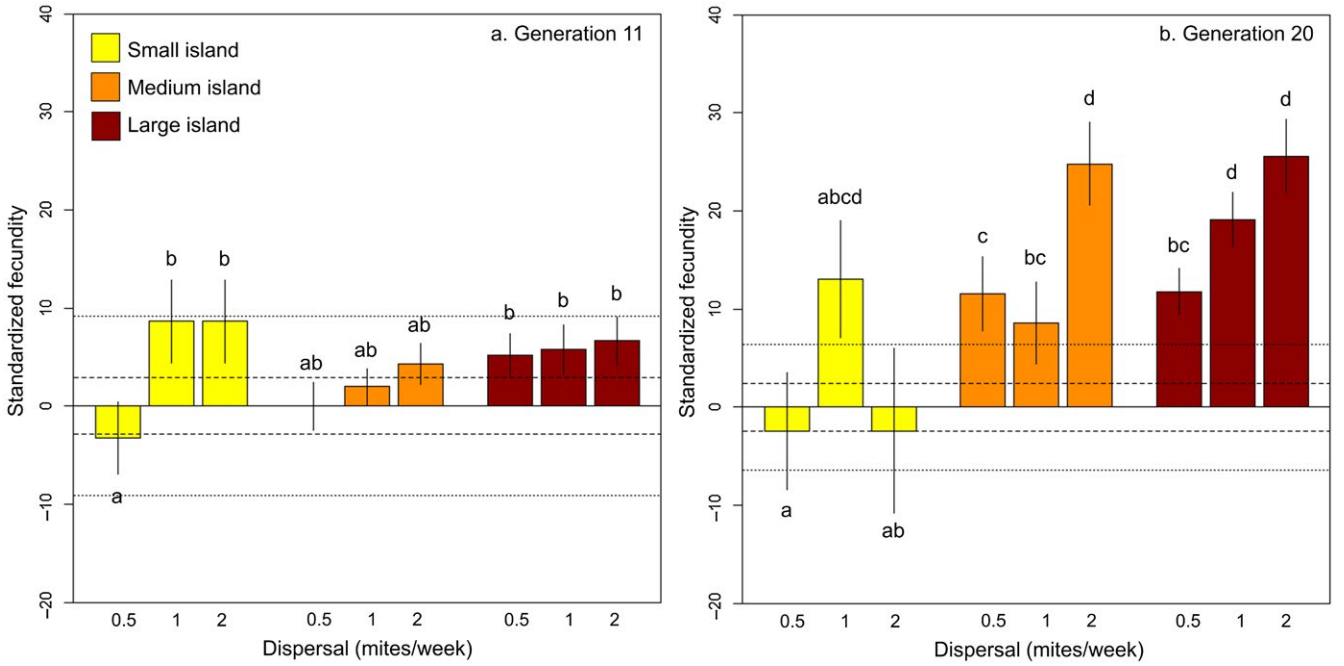


**FIGURE 5** Effect of island size and dispersal on female fecundity after 11 (a) and 20 (b) generations of adaptation to tomato. After 11 generations, none of the populations that had been evolving on tomato plants was more adapted to tomato than the mainland population. After 20 generations, populations from three treatments were better adapted to tomato plants than the mainland population: those evolving on medium-sized islands receiving the largest dispersal (2 mites/week) and the populations evolving on large islands receiving 1 and 2 mites/week. Fecundity was standardized by subtracting the mean fecundity of female mites coming from the mainland from the fecundity of the female mites coming from the islands. Dotted and dashed lines show, respectively, the standard deviation and the standard error of the fecundity of the mainland mites. Differences between dispersal–island size treatments are indicated with letters

also explains the differences in which are reduced with a decrease in island size and dispersal. From our experiment, we can infer the nature of the relationship between extinction and isolation/dispersal (as put forward by Patiño et al., 2017) for single populations, but it is likely that similar principles also apply at a community level.

In a similar manner to extinction events, colonization time is affected by dispersal and island size. Island colonization rate is highest in populations receiving the largest number of immigrants, irrespective of island size, and this suggests a positive effect of dispersal on demographic and genetic rescue. For high isolation, with low dispersal constraining demographic and genetic rescue, island size does matter for successful colonization. This is likely to be attributable to the fact that larger islands offer more resources and populations can grow to large numbers, reducing demographic stochasticity and thus extinction. Thus, for successful colonization to occur, populations on large islands do not require a large number of dispersal events. On small islands, colonization occurs early when dispersal is high, but these populations are unlikely to be self-sustainable and may act as sink populations that are likely to go extinct when disconnected from the mainland immigration.

Our experiment shows that small islands do not allow for local adaptation, because population sizes are too small and the chances of extinction too high. Even when extinction events on small islands are countered by frequent immigration, local adaptation is never achieved, probably owing to a genetic load effect. Furthermore, the small population size on small islands may negatively affect the adaptive capacity of populations owing to increased inbreeding, genetic drift (Ellstrand & Ellam, 1993) and historical contingency (Lachapelle et al., 2015).

MacArthur and Wilson (1967) also suggested a negative effect of dispersal on adaptation: 'near the outer limit of the dispersal range of a given taxon speciation and exchange of newly formed autochthonous species within an archipelago can outrun immigration from outside the archipelago and lead to the accumulation of species on single islands. Despite their common origin, such species tend to be adaptively quite different from each other, and the result is adaptive radiation in the strict sense' (p. 180). Negative relationships between dispersal and adaptation have been reported for both empirical and experimental studies (Alzate et al., 2017; Bolnick & Nosil, 2007; Cuevas et al., 2003). Such negative relationships might be attributable to genetic load or to a decrease in fitness resulting from exceeding the carrying capacity (Garant et al., 2007). Nevertheless, theoretical studies suggest that the effects of dispersal on local adaptation are not inevitably negative, but can also be positive (e.g., because of demographic and genetic rescue effects; Blanquart et al., 2012; Garant et al., 2007; Holt & Gomulkiewicz, 1997). These factors reduce extinction by replenishing population density and increasing genetic variation (Lenormand, 2012). Such positive effects may be especially

important for populations living in marginal habitats or at the edge of the species range (Brown & Kondric-Brown, 1977; MacArthur & Wilson, 1967), because dispersal may allow these populations to persist long enough to make evolutionary change possible (Holt & Gomulkiewicz, 1997; Kawecki, 1995). However, so far there has been very little empirical evidence for the positive effects of dispersal on adaptation. A notable exception can be found for bacteriophages (Ching et al., 2012), for which intermediate levels of dispersal were related to maximum adaptation. Here, we expand upon these findings by showing positive effects of dispersal on local adaptation of the two-spotted spider mite to a new host plant. Previously, it has been shown that when dispersal events are even more frequent than studied here, its effects can reverse and become negative (Alzate et al., 2017); therefore, we expect that there is an optimal level of isolation (dispersal) for which adaptation reaches a maximum. We argue that populations on an island too close to the mainland would not be able to differentiate from the mainland population owing to high genetic load. Likewise, populations on an island too distant from the mainland would probably not be able to adapt, because there are insufficient migration events to provide the genetic variation needed for natural selection to act on. At intermediate levels of dispersal, populations are not too isolated to be deprived from genetic variability and not too connected to be overloaded with maladapted individuals from the mainland, so that opportunities for local adaptation are expected to be highest. However, if we want to extrapolate our findings to the real world, other factors should be taken into account. For instance, the geological time effect, which could not be included in our experiment, means that the conditions on real islands (oceanic islands) are not constant over time (Borregaard et al., 2017). Therefore, island area and heterogeneity can vary over time, and with this the opportunities for adaptation and island species richness (via immigration for less isolated islands or via speciation for isolated islands).

Given the current global situation of habitat fragmentation and loss, where many populations are becoming smaller and more isolated (Fahrig, 1997; Wiegand, Revilla, & Moloney, 2005), an understanding of the effects of habitat size and isolation on the eco-evolutionary dynamics, colonization success and extinction of populations is vital for better management and conservation efforts. To the best of our knowledge, our study is the first to show experimentally the interactive effects of habitat size and migration on both extinction and colonization events (via demographic and genetic rescue), and on local adaptation to the new habitat. In spite of the limitations of microcosm experiments (e.g., their simplicity, hence their idealized representation of nature), they can also provide valuable insights about patterns and processes in a larger real-world setting (Drake & Kramer, 2012; Gonzalez, Lawton, Gilbert, Blackburn, & Evans-Freke, 1998; Lawton, 1999). They present a more tractable way to study complex biological systems, while keeping a focus on the factors of interest and allowing for repeatability (Lawton, 1996, 1999). Therefore, this type of experimental biogeography can provide important insights into the ways in which populations can respond to fragmentation and habitat loss at an ecological and evolutionary level. As such, our study provides a key step in incorporating microevolutionary processes into IBT. Ultimately, incorporating such processes is necessary for understanding how new species might arise in isolated habitats, and thus how both present-day and future large-scale biodiversity patterns arise and are altered by drivers of global change.

## 5 | DATA ACCESIBILITY

Data used in this study are available on the DataverseNL digital repository: https://hdl.handle.net/10411/PGTUCQ


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## BIOSKETCH

**Adriana Alzate** is interested in ecology, evolution and macroecology, particularly in how eco-evolutionary dynamics can shape macroecological patterns.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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