



Local extinction risk under climate change in a neotropical asymmetrically dispersed epiphyte

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Abstract

1. The long-term fate of populations experiencing disequilibrium conditions with their environment will ultimately depend on how local colonization and extinction dynamics respond to abiotic conditions (e.g. temperature and rainfall), dispersal limitation and biotic interactions (e.g. competition, facilitation or interactions with natural enemies). Understanding how these factors influence distributional dynamics under climate change is a major knowledge gap, particularly for small ranged and dispersal-limited plant species, which are at higher risk of extinction. Epiphytes are hypothesized to be particularly vulnerable to climate change and we know little about what drives their distribution and how they will respond to climate change. To address this issue, we leveraged a 10-year dataset on the occupancy dynamics of the endemic orchid *Lepanthes rupestris* to identify the drivers of local colonization and extinction dynamics and assess the long-term fate of this population under multiple climate change scenarios.
2. We compared 290 dynamic occupancy models in their ability to predict the colonization and extinction dynamics of a *L. rupestris* metapopulation. The model set predicted colonization–extinction dynamics as a function of asymmetric patch connectivity, moss area, elevation, temperature (minimum, maximum and variability) and/or rainfall.
3. The best model predicted that local colonization increases with increasing asymmetric patch connectivity but decreases as minimum temperature and maximum temperature variability increase. The best model also predicted that local extinction increases with increasing variability in maximum temperature. Negative effects were more severe in smaller patches.
4. *Synthesis*. Overall, our results demonstrate the role of asymmetric connectivity, climate and interactions with moss area as drivers of colonization and extinction dynamics. Moreover, our results suggest that asymmetrically dispersed epiphytes may struggle to persist under climate change because their limited connectivity may not be enough to counterbalance the negative effects of increasing mean or variability in temperature.

KEYWORDS

biotic interactions, climate change, colonization, connectivity, epiphytes, extinction, *Lepanthes rupestris*, Puerto Rico

1 | INTRODUCTION

Identifying the drivers of species distributions is a central challenge in ecology and evolutionary biology, particularly within the context of global climate change (Gaston, 2009). Historical data and fossil records provide ample evidence that climate is a major driver of species distributions over long temporal scales (Davis & Shaw, 2001; Holdridge, 1947). At shorter temporal scales, empirical evidence demonstrates that changes in climate are currently driving rapid shifts in species distributions (Parmesan & Yohe, 2003) as well as range expansions and contractions (e.g. Hughes, 2000). While changes in climate are a major driver of distributional dynamics, observed dynamics are often the result of complex interactions between climate, biotic interactions and dispersal behaviour (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010; Travis et al., 2013). Understanding the mechanisms through which these factors influence distributional dynamics under climate change is a major knowledge gap, particularly for small ranged and dispersal-limited species which are at high risk of extinction (Davies, Margules, & Lawrence, 2004).

What happens to plant populations when the climate changes beyond a species' thermal tolerance zone? Plant populations can adapt and persist locally (e.g. Franks, Sim, & Weis, 2007). Other populations may shift their range colonizing sites with more favourable conditions (e.g. Kelly & Goulde, 2008). Alternatively, plant populations can decline and ultimately go locally extinct due to physiological constraints or unfavourable biotic interactions (Wiens, 2016). Globally, models predict that around 6% of all plant species are at risk of extinction due to climate change (Urban, 2015). Mountain systems in the neotropics are particularly vulnerable with approximately 9% of species at severe risk of extinction (Dirnböck, Essl, & Rabitsch, 2011; Dullinger et al., 2012). Many mountain-dwelling populations are moving upwards in elevation (Lenoir & Svenning, 2015), but the success of moving populations will depend on a plant's ability to disperse and adapt to novel biotic and abiotic conditions on the expansion front (Parmesan, 2006; Pearson & Dawson, 2003; Primack & Miao, 1992).

Dispersal determines the rate at which population ranges can change (Bell & González, 2011). Active dispersers may be able to compensate for moderate disequilibrium conditions with climate through behavioural modifications (e.g. McCain & King, 2014). In contrast, range shifts in passive dispersers are limited because they depend on biotic or abiotic agents for dispersal (Wares, Gaines, & Cunningham, 2001). Dispersal limitation is greater for passively dispersed plants that depend on asymmetric advection sources such as wind or water for long-distance dispersal. The additional restriction from asymmetric dispersal can limit species' range boundaries

and result in higher risks of local extinction (Sorte, 2013). With few exceptions (see Nathan et al., 2011), we know little about how asymmetrically dispersed plant populations will respond to climate change. Moreover, we know less about the effects of asymmetric dispersal on responses to climate change in understudied plant groups, such as epiphytes.

Epiphytes comprise 10% of all global plant species and more than 25% of all tropical vascular plants (Nieder, Prosperí, & Muchaloud, 2001). This diverse group of plants is hypothesized to be particularly vulnerable to climate change due to their dependence on moisture from the atmosphere (del Castillo, Trujillo-Argueta, Rivera-García, Gómez-Ocampo, & Mondragón-Chaparro, 2013). Also, epiphytes often disperse among substrates passively through asymmetric advection sources, which limit their potential to respond to climate change through range shifts (Dettki, Klintberg, & Esseen, 2000; Werth et al., 2006). These responses to climate change will also depend on how changes in temperature and rainfall influence the tight relationship with their host plants. The cross-scale effect of plant-plant interactions on ecological dynamics are beginning to be recognized, but still we know little about the potential role of facilitation driving species distributions under climate change (Soliveres & Maestre, 2014). Moreover, there is little empirical work assessing the vulnerability of epiphytes to climate change. Moreover, there is little empirical work assessing the factors determining epiphyte responses to climate change. The few pattern-based studies show large negative effects including 93% predicted distributional loss for lichen species in the Appalachians (Allen & Lendemer, 2016), shifts in species composition of lichens and bryophytes of the alpine spruce forest (Nascimbene & Spitale, 2017) and reduced leaf production and longevity in tropical epiphyte mats in Costa Rica (Nadkarni & Solano, 2002). Still, we know little about the factors that could drive shifts in epiphyte species distributions under climate change.

Few studies incorporate biological information on species-specific dispersal abilities or species interactions when studying potential responses to climate change (Record et al., 2018). Furthermore, many forecasts of future species distributions are derived from simple occupancy-environment relationships that are limited because they analyse data on distributional patterns from a single snapshot in time which makes the simplifying assumption of spatiotemporal equilibrium (Araújo & Peterson, 2012). An alternative is to model local colonization and extinction, which are the processes that generate distributional shifts over time. Local colonization and extinction can be modelled as a function of climatic variables using process-based approaches that leverage time-series data (Dornelas et al., 2013; Yackulic, Nichols, Reid, & Der, 2015) and directly incorporate dispersal potential and species

interactions in modelled estimates (Acevedo, Fletcher, Tremblay, & Melendez-Ackerman, 2015).

In this study, we leverage a 10-year dataset on a spatially structured population of the asymmetrically dispersed orchid *Lepanthes rupestris*, to ask, to what extent do climate, dispersal potential and local habitat characteristics (i.e. patch area and phorophyte type) drive local colonization–extinction dynamics in this epiphyte population? In the long term, will the population persist, shift or decline towards extinction? Understanding the relative contributions of dispersal potential, abiotic factors and local habitat characteristics to

local colonization–extinction dynamics will fill an important gap in our knowledge of distributional responses to climate change by epiphytes.

2 | MATERIALS AND METHODS

2.1 | Study system

Our study species, *L. rupestris*, is an orchid endemic to the Puerto Rico mountains (Figure 1; Ackerman, 1995). It is mostly found on

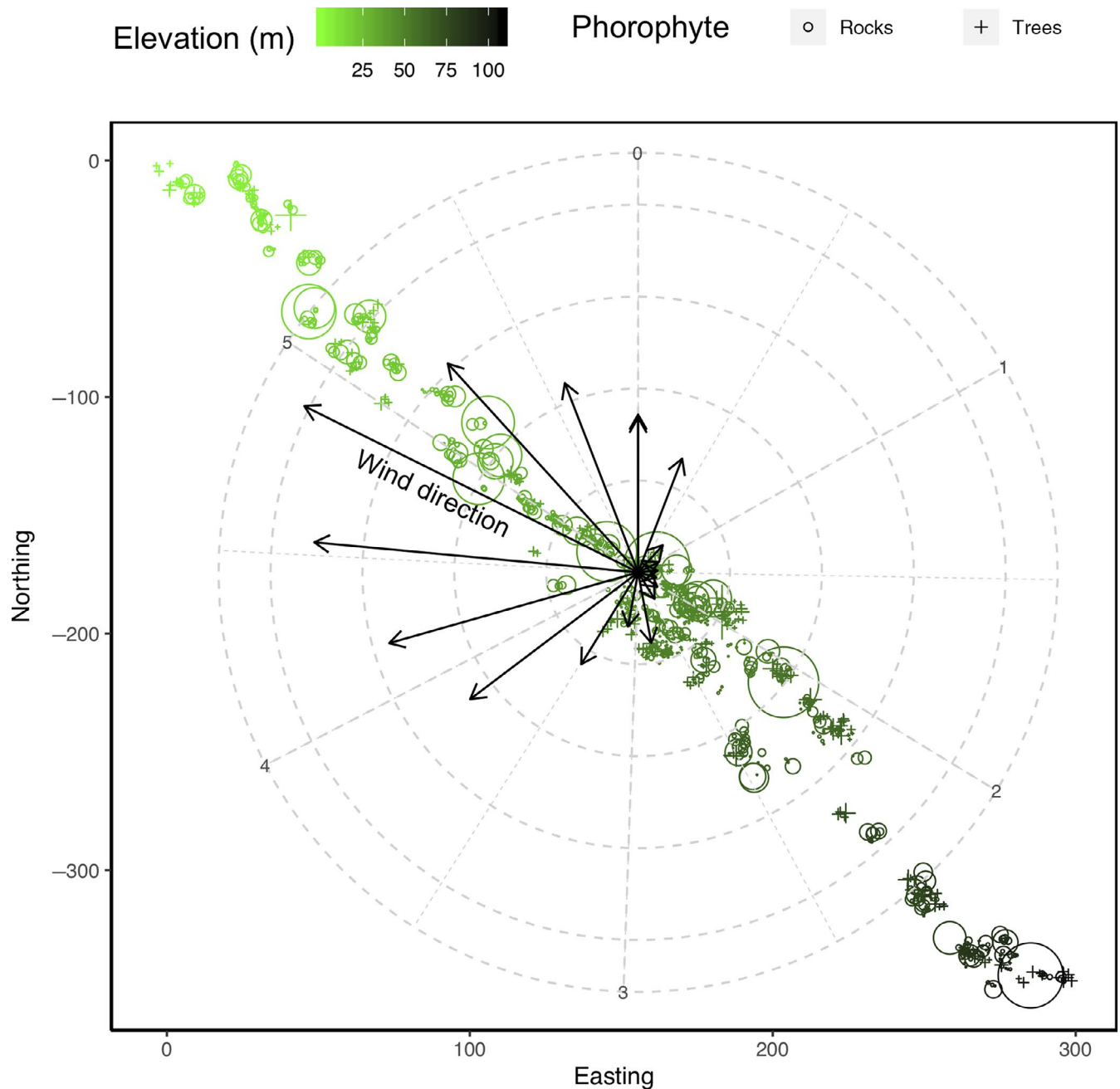


FIGURE 1 Map showing the spatial arrangements of local populations of *Lepanthes rupestris* in rocks (grey points) and tree (black crosses) phorophytes in Quebrada Sonadora—a first-order tributary of the Espíritu Santo River in the Luquillo Experimental forest (US Department of Agriculture Forest Service). The overlaid circular histogram shows the distribution of wind direction (in radians) during the study period. The relative size of the symbols represents moss area in the phorophyte

the western slope the Luquillo Experimental Forest between 200 and 9,025 m in elevation. There is literature suggesting that the species may be found elsewhere in Puerto Rico, specifically in Sierra de Cayey and La Torrecilla in the Cordillera Oriental (Axelrod, 2011). Yet, the current status, size and population trends of these two populations have not been assessed.

The orchid *L. rupestris* anchors its roots in moss living on rock or tree phorophytes; biological interactions with moss are key because moss provides physical structure, moisture and nutrients for the orchid (García-Cancel et al., 2013). Moss species used by *L. rupestris* vary but most belong to the families Calymperaceae, Thuidiaceae and Sematophyllaceae (García-Cancel et al., 2013). The orchid is small (leaves <4.3 cm, shoots <15 cm of height) with an average life span of 3.4 years (Tremblay, 2000) and has low reproductive rates due to infrequent pollination events (Tremblay, 1997). The seeds are wind-dispersed with a mean dispersal distance of 4.8 m; dispersal occurs asymmetrically because of wind directionality (Acevedo et al., 2015). An asymmetric measure of connectivity that accounts for wind direction is most appropriate to describe patch connectivity (see below; Acevedo et al., 2015). Potential effects of seed banks on the dynamics of this species are likely negligible because seeds do not have endosperm. Seeds are not viable when they come in contact with water or bare soil (Tremblay, Meléndez-Ackerman, & Kapan, 2006).

To assess the drivers of colonization and extinction dynamics on this species, we used presence/absence data on a permanent plot (18°18'N, 65°47'W) of 975 mapped occupied and non-occupied patches (either rock or tree phorophytes). These patches were surveyed twice a year (winter and summer) from 1999 to 2008. The total moss area was estimated in each patch using a 150 cm² grid. See Tremblay et al. (2006) for details on plot establishment and design.

Environmental variables were extracted from a nearby weather station (<300 m) located at El Verde field station (Ramírez & Meléndez-Colom, 2003). These data included average daily variation in wind direction, minimum temperature, maximum temperature and rainfall. Wind data were not available for the years 1999, 2000 and 2005; hence, we used the average value for the whole period to calculate the asymmetric dispersal measure for these years (see below). To characterize temperature and rainfall during the sampling periods, we used 6-month averages prior to the survey to be consistent with the demographic closure assumptions of the dynamic occupancy model used to estimate local colonization and extinction probabilities (see below). To estimate the number of dry days, we calculated the number of days without precipitation in the 6 months before each survey.

2.2 | Dynamic occupancy modelling

We used dynamic (multi-season) occupancy modelling to estimate colonization and extinction probabilities as a function of covariates (phorophyte type, asymmetric connectivity, elevation, rainfall,

minimum temperature, maximum temperature, variability in temperature, number of dry days and moss area). Dynamic occupancy models are an appropriate alternative to incidence function models (Hanski, 1999) in instances when detection is imperfect and the Markovian pseudoequilibrium assumption cannot be tested. This modelling approach follows Pollock's robust design sampling design composed of two sampling periods. Colonization and extinction parameters are estimated among primary periods, which are assumed to be demographically open. Secondary periods take place within primary periods and are used to estimate the probability of detection. The system is assumed to be closed between these secondary periods (see Rota, Fletcher, Dorazio, & Betts, 2009). Years (1999–2008) characterize our primary periods ($n = 10$). Our secondary periods are characterized by the two censuses (January–February and July–August) that were conducted each year. Within this sampling design, the system is assumed open for colonization and extinction during the wet season where tropical storms are common and likely responsible for most local extinction and strong wind gusts likely responsible for many local colonization events (Tremblay et al., 2006). While we expect detectability to be high, it may be imperfect in small patches where it will be difficult to discern between moss and a small individual (Acevedo et al., 2015). We fit all models using maximum likelihood and the L-BFGS-B optimization procedure as developed in the R package UNMARKED.

We estimated asymmetric patch connectivity ($C_{i,t}$) for patch i and year t using the approach developed by Acevedo et al. (2015):

$$C_{i,t} = \sum_{j \neq i}^N \exp\left(-\alpha \frac{d_{ij}}{1 - \delta_{ij,t}}\right) p_{j,t} A_j,$$

where N represents the total number of patches (both occupied and unoccupied) in the landscape, $1/\alpha$ is the average dispersal distance of the species (i.e. 4.8 m), and d_{ij} describes the Euclidean distance between patches i and j . The parameter $\delta_{ij,t}$ describes the difference between the angle of wind direction and the angle between patches i and j with respect to the horizontal axis. We scaled this parameter by π to have the constrain $\delta_{ij,t} \in [0,1]$. The parameter p_j represents the naive occupancy state of patch j in year t and A_j represents moss area of patch j . Note that in this case moss area is used as a proxy for the population size of patch j .

To test for the factors driving distributional dynamics in *L. rupestris*, we followed a multiple competing hypotheses approach (Chamberlin, 1965). This approach is an alternative to single hypothesis falsification (Popper, 1935). The advantage of the multiple competing hypotheses approach is that it allows for the possibility of more than one hypothesis having similar support explaining an observed phenomenon (Betini, Avgar, & Fryxell, 2017; Elliot & Brook, 2007). We operationalized this approach by using AIC to compare multiple a priori hypotheses described by a model. The most parsimonious model (or hypothesis with the strongest support) would have the lowest AIC. In the case of two or more models having $AIC < 2$, we used model averaging and made inference on the averaged model (Burnham & Anderson,

2004). For model averaging, these top models were assigned equal weights.

We compared 290 models in their ability to describe *L. rupestris* colonization and extinction dynamics. Each model represented a priori hypotheses about what covariates influence initial occupancy (ψ), detectability (p), colonization (γ) and extinction (ϵ ; Supporting Information S1). We included phorophyte type as a covariate for all variables because rocks are more likely to be occupied than tree phorophytes (Tremblay et al., 2006). We also included moss area and phorophyte type as covariates for the probability of detection (p) in all models because this orchid may be difficult to detect in small phorophytes.

We compared four types of models. (a) Null models: We fit two null models which included an intercept-only model with no covariates for any of the response variables and another with phorophyte type as a covariate for initial occupancy and patch area and phorophyte type as covariates for the probability of detection. These null models represented hypotheses predicting no relationship between colonization or extinction and asymmetric connectivity, abiotic factors or moss area. (b) Single effect of abiotic factors: We fit models in which the single effect of maximum temperature, minimum temperature, variation in minimum temperature, variation in maximum temperature, rainfall, number of dry years and elevation influenced colonization, extinction or both. (c) Target effects model: Previous studies have shown that the colonization-extinction dynamics in this system was best predicted by a model that included asymmetric connectivity and moss area as covariates for local colonization (target effects model) and moss area as a covariate for local extinction (Acevedo et al., 2015). This model represents the hypothesis that the colonization-extinction dynamics in this system are better predicted by a combination of spatial attributes and moss area. (d) Combined models: We fit models that combined one or two abiotic factors, with moss area and/or asymmetric connectivity as covariates for colonization and one or two abiotic factors with moss area as covariates for extinction. These models represent hypotheses that predict that colonization and extinction dynamics are best predicted by combined effects of asymmetric connectivity, moss area or abiotic factors (Supporting Information S1). We also tested for an interaction between moss area and abiotic factors to test the hypothesis that the effect of abiotic factors may vary by patch size.

2.3 | Equilibrium occupancy and future projections

We estimated equilibrium occupancy to assess the long-term asymptotic proportion of patches expected to be occupied if colonization and extinction rates remain constant. To estimate equilibrium occupancy (ψ^*), we used estimated colonization (γ) and extinction (ϵ) parameters from the averaged model such that $\psi^* = \gamma/(\gamma + \epsilon)$ (Ferraz et al., 2007). Assessing the future fate of the population using equilibrium occupancy follows a conservative approach making a single assumption of asymptotic equilibrium. An alternative approach

would be to use the model to predict future yearly probabilities of occupancy, which would require making multiple assumptions about the temporal variability of abiotic and biotic factors that are difficult to test. Instead, our conservative approach using equilibrium occupancy simply assesses what would be the asymptotic occupancy rate without making assumptions about temporal variability. If rainfall or temperature are important covariates for local colonization, extinction or both, we can estimate equilibrium occupancy using predicted colonization and extinction rates under multiple climate change scenarios.

We operationalized population persistence, shifts and declines based on the following expectations. If *L. rupestris* persists locally in the long term, predicted occupancy at equilibrium would be similar or higher to the predicted occupancy under current conditions. If the population shifts, elevation would be a covariate in the best model for colonization, extinction or both; predicted changes in occupancy that varied with elevation would suggest distributional shifts. Lastly, if *L. rupestris* declines in the long term, predicted equilibrium occupancy under future conditions would be smaller than under current conditions; we would expect extinction as predicted equilibrium occupancy approaches <0.001.

Downscaled general circulation models for Puerto Rico predict increases in temperature of 4.6–9°C by 2099, which are 1–3°C higher than global predictions, with temperature extremes projected to increase at a similar rate (Khalyani et al., 2016). Similarly, downscaled models predict that annual daily variance in minimum and maximum temperature will also increase 2.10–3°C depending on the amount of temperature increase predicted. For our predictions, we used a variance of 2.72 which is a conservative estimate for a temperature increase of 2°C over the global estimates (Hayhoe, 2013). These scenarios also predict annual decreases in rainfall of 312.57–510.67 mm (Khalyani et al., 2016). Our approach allows us to address the question: If mean or variability in temperature or rainfall changes following climate change projections, what will be the proportion of occupied patches in the long term if the predicted local colonization and extinction probabilities remain constant through time?

3 | RESULTS

Of the 290 models compared, two were the most parsimonious in explaining the colonization and extinction dynamics of *L. rupestris* ($\Delta AIC < 2$, combined $AIC_{wt} = 0.73$; Table 1). The best model included phorophyte type, asymmetric connectivity and an interaction between moss area and minimum temperature as covariates for colonization. This model also included phorophyte type, and moss area interacting with variability in maximum temperature as covariates for extinction (Supporting Information S2). The next best model ($\Delta AIC = 0.88$) included similar covariates for extinction, but it included an interaction between moss area and variability in maximum temperature as covariates for colonization instead of an interaction with minimum temperature (Table 1; Supporting Information S3). These models suggest that connectivity, temperature and patch area

TABLE 1 Model comparison of dynamic occupancy models predicting initial occupancy (ψ), colonization (γ) and extinction (ϵ) as function of asymmetric connectivity (AsymConn), moss area (A), phorophyte type (Ph), rainfall (Rain), minimum temperature (MinTemp) and maximum temperature (MaxTemp). The most parsimonious models ($dAIC < 2$) included connectivity, moss area and phorophyte type for colonization and extinction. The table also reports number of parameters (k) and model weight (AICwt). Note that the table is sorted by $dAIC$, and for simplicity, we show only the top eight ranked models and the two null models (see Supporting Information S1 for the full table). We made inferences on the averaged model between the best two (highlighted in bold)

Model	k	$dAIC$	AIC _{wt}
ψ (Ph) γ (AsymConn + Ph + A*<i>mintemp</i>) ϵ (Ph + A*<i>var_max</i>) p (A + Ph)	16	0	0.44
ψ (Ph) γ (AsymConn + Ph + A*<i>var_max</i>) ϵ (Ph + A*<i>var_max</i>) p (A + Ph)	16	0.88	0.29
ψ (Ph) γ (AsymConn + Ph + A* <i>var_rain</i>) ϵ (Ph + A* <i>var_max</i>) p (A + Ph)	16	2.92	0.106
ψ (Ph) γ (AsymConn + A + Ph) ϵ (Ph + A* <i>var_max</i>) p (A + Ph)	14	3.73	0.07
ψ (Ph) γ (AsymConn + Ph + A* <i>var_min</i>) ϵ (Ph + A* <i>var_max</i>) p (A + Ph)	16	3.83	0.07
ψ (Ph) γ (AsymConn + Ph + A* <i>rain</i>) ϵ (Ph + A* <i>var_max</i>) p (A + Ph)	16	5.58	0.03
ψ (Ph) γ (Ph + A* <i>mintemp</i>) ϵ (Ph + A* <i>var_max</i>) p (A + Ph)	15	10.63	0.002
ψ (Ph) γ (Ph + A* <i>var_max</i>) ϵ (Ph + A* <i>var_max</i>) p (A + Ph)	15	10.78	0.002
ψ (Ph) γ (.) ϵ (.) p (A + Ph)	7	75.48	<0.01
ψ (.) γ (.) ϵ (.) p (.)	4	117.82	<0.01

are important drivers of *L. rupestris* colonization–extinction dynamics. Furthermore, these results suggest little evidence for elevation as a key predictor.

The averaged model predicts that the probability of detection was high ($0.85\text{--}0.99 \pm 0.01$ SE) and it increased with increasing moss area (Supporting Information S4). The averaged model also predicts that the odds of local colonization were 2.10 (± 0.54 SE) times more likely in trees than rock phorophytes and that the odds of local extinction in trees were 0.97 (± 0.28 SE) times those of rocks.

The averaged model predicts that the probability of colonization increases with patch connectivity but decreases with increasing minimum temperature or variability in maximum temperature. This negative effect of temperature on local colonization was slightly higher in smaller patches. The odds of local colonization increase 1.42 (± 0.13 SE) times with a unit increase in asymmetric patch connectivity (Figure 2). Also, the odds of local colonization increase 1.65 (± 0.13 SE) times with a unit increase in moss area. The odds of local colonization decrease 0.66 (± 0.11 SE) times with an increase of one unit of minimum temperature (Figure 3). Yet, the effect of the interaction with minimum temperature and moss area predict that these odds change an extra 0.92 (± 0.06 SE) with a unit change in moss

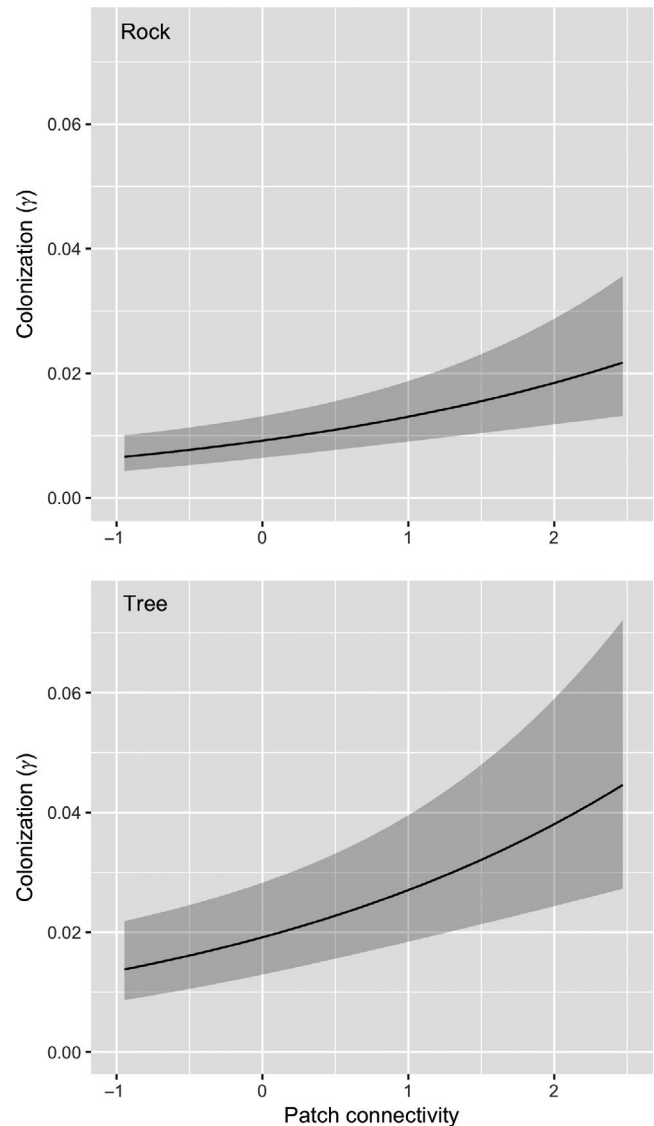


FIGURE 2 Partial relationships between asymmetric patch connectivity and probability of colonization from the averaged model. The model predicts that local colonization probability increases with increasing asymmetric patch connectivity in both phorophytes

area. Similarly, the averaged model predicts that the odds of local colonization decrease 0.62 (± 0.15 SE) times with a unit increase in variation in maximum temperature. Yet, the effect of the interaction with moss area predicts that these odds change 1.14 (± 0.09 SE) times with a unit change in moss area. For example, in rock phorophytes, the predicted probability of local colonization in large patches (75th percentile) under high variability in maximum temperature (75th percentile) is slightly higher (0.009 ± 0.002 SE) than the predicted probability of colonization in smaller patches (25th percentile; 0.007 ± 0.002 SE; Figure 3). Similarly, in tree phorophytes, the predicted probability of local colonization in large patches under high variability in maximum temperature is slightly higher (0.02 ± 0.006 SE) than the predicted probability of colonization in smaller patches (0.01 ± 0.004 SE; Figure 3).

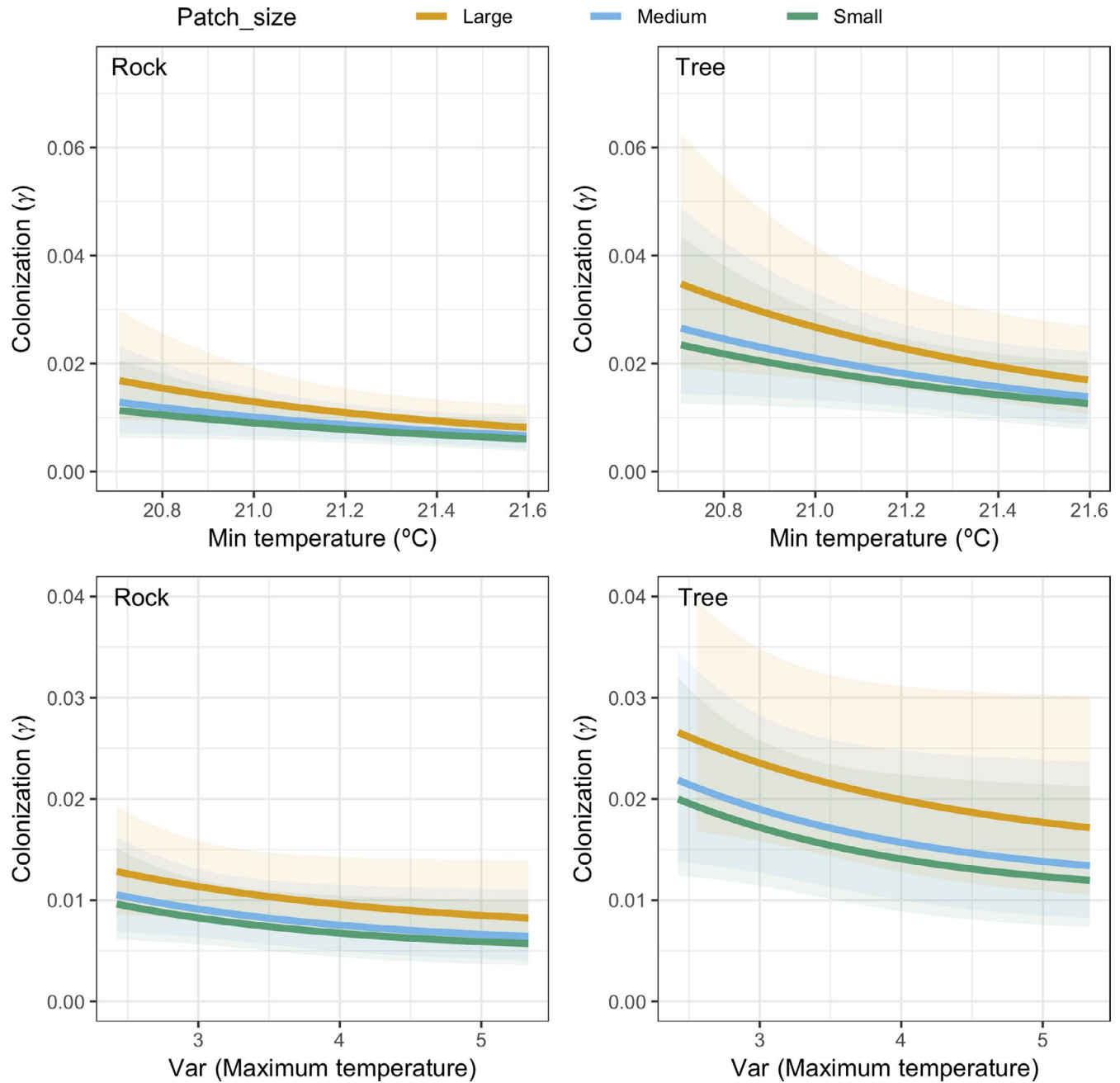


FIGURE 3 Partial relationships between local colonization and moss area interacting with minimum temperature and variability in maximum temperature. The averaged model predicts that local colonization decreases with increasing minimum and variability in maximum temperature. This decrease in colonization is more severe in smaller patches and the relationship is consistent for both phorophyte types. Small patches are represented by the 25th percentile, medium patches by the 50th and large patches by the 75th percentile of the distribution of patch sizes

The averaged model predicted that local extinction decreases with increasing variability in maximum temperature in larger patches but increases in medium or small patches (Figure 4). The odds of local extinction decrease 0.13 (± 0.06 SE) times with a unit increase in patch area for an average effect of variability in maximum temperature. Similarly, the odds of local extinction decrease 0.81 (± 0.19 SE) times with a unit increase in the variability of maximum temperature for an average effect of moss area. Yet, the effect of the interaction predicts that these odds change 0.19

(± 0.08 SE) times with a unit change in moss area. For example, the predicted probability of local extinction under high variability in maximum temperature for a small patch (25th percentile) is 0.09 (± 0.02 SE), while the predicted probability of local extinction for a large patch (75th percentile) is 0.02 (± 0.01 SE).

The averaged model predicted that equilibrium occupancy of large tree phorophytes will decrease from $\psi^*_{\text{TREE,L}} = 0.50$ under current conditions to $\psi^*_{\text{TREE,L}} = 0.26$ under the most severe climate change scenario (A2) by 2099. A similar pattern is predicted for large

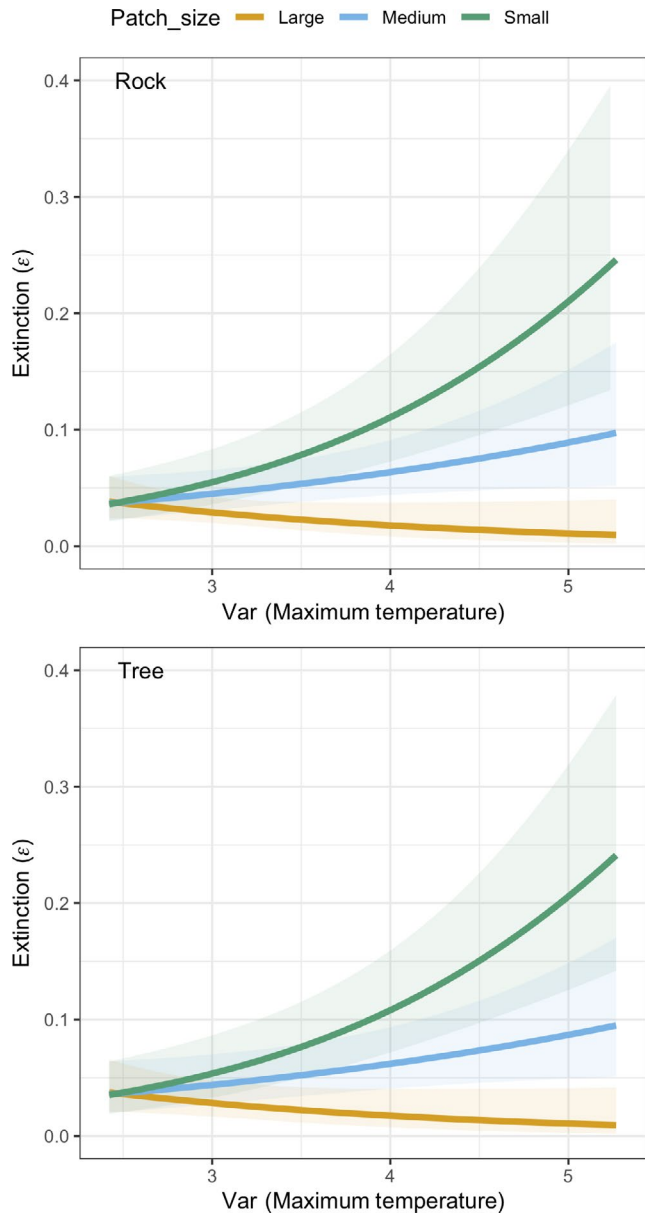


FIGURE 4 Partial relationships between local extinction and variability in maximum temperature interacting with moss area. The model predicts that local extinction increases as variability in maximum temperature increases. This effect is predicted to increase as moss area declines. Small patches are represented by the 25th percentile, medium patches by the 50th and large patches by the 75th percentile of the distribution of patch sizes

rock phorophytes where equilibrium occupancy is predicted to decrease from $\psi_{\text{ROCK,L}}^* = 0.31$ to $\psi_{\text{ROCK,L}}^* = 0.14$ (Figure 5). The predicted decrease in equilibrium occupancy is more severe for small patches. The averaged model predicted that equilibrium occupancy of small tree phorophytes will decrease from $\psi_{\text{TREE,S}}^* = 0.19$ to $\psi_{\text{TREE,S}}^* < 0.001$ (<1 patch occupied at equilibrium) under the most severe climate change scenario (A2) by 2099. A similar pattern is predicted for small rock phorophytes where equilibrium occupancy is predicted to decrease from $\psi_{\text{ROCK,L}}^* = 0.10$ to $\psi_{\text{ROCK,L}}^* < 0.001$ (<1 patch occupied at equilibrium; Figure 5).

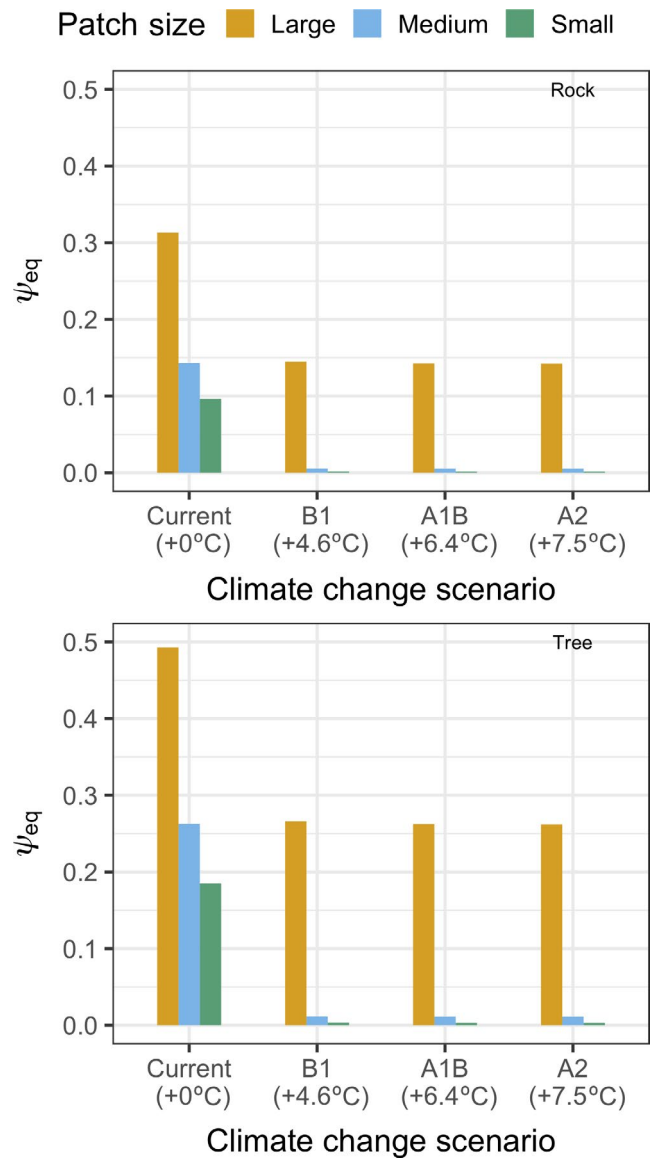


FIGURE 5 Predicted equilibrium occupancy (ψ_{eq}) under three 2099 climate scenarios. Equilibrium occupancy describes the asymptotic number of occupied patches if colonization and extinction rates remain constant through time. The 'current' scenario represents equilibrium occupancy based on current conditions. Scenarios B1, A1B and A2 represent downscaled general circulation models for Puerto Rico (Khalyani et al., 2016). These are sorted from the most conservative to the scenario that predicts the highest temperature increase. Small patches are represented by the 25th percentile medium patches by the 50th and large patches by the 75th percentile of the distribution of patch sizes

4 | DISCUSSION

We know little about the effects of dispersal limitation, spatial attributes and climate driving plants distributional shifts (Record et al., 2018). This is particularly true for epiphytes that compose a significant proportion of all plant species, have a disproportionately large effect on ecosystem processes but are critically understudied. We

leveraged a 10-year dataset on the occupancy dynamics of the endemic orchid *L. rupestris* to identify the drivers of local colonization and extinction dynamics (the processes that generate species distributions) and assess if this spatially structured population will persist, shift or go extinct under multiple climate change scenarios. We found that local colonization increases with increasing asymmetric connectivity but decreases with increasing minimum temperature and variability in maximum temperature. We also found that local extinction increases with increasing variability in maximum temperature. These effects were most severe in smaller patches. Overall our results suggest an unbalance between colonization and extinction that may ultimately result in a decline in equilibrium occupancy in large patches and extinction in smaller patches by 2099 under all climate change scenarios.

Our results emphasize asymmetric connectivity as an important driver of local colonization. Classical metapopulation theory emphasizes the role of connectivity as a driver of colonization and extinction dynamics, and persistence (Hanski, 1999). While there is some empirical evidence supporting the importance of connectivity for persistence (e.g. Damschen et al., 2019), there are also studies that show contradicting evidence (e.g. Kindlmann, Meléndez-Ackerman, & Tremblay, 2014). Indeed, a literature synthesis found that connectivity was an important predictor in only a handful of all studies analysed (Pellet, Fleishman, Dobkin, Gander, & Murphy, 2007). Variability in empirical support for the role of connectivity and colonization–extinction dynamics may be a consequence of applying connectivity measures that assume symmetric dispersal when dispersal is likely asymmetric (Acevedo & Fletcher, 2017). Models that assume symmetric dispersal often fail to account for density-independent movements that are common in many organisms (Acevedo et al., 2015). Accounting for asymmetric connectivity is an appropriate alternative for many systems.

The relationship between temperature, and colonization–extinction dynamics in *L. rupestris* may be explained by the mechanisms by which temperature influences establishment and reproduction. Laboratory experiments show that *Phalaenopsis* orchid inflorescence production peaks at temperatures lower than 23°C and is inhibited when temperature exceeds 27°C (Blanchard & Runkle, 2006; Goh & Arditti, 1985). In *L. rupestris*, fruit production increases with optimal lower temperatures leading to increasing inflorescence and flower production that attracts more pollinators (Olaya-Arenas, Meléndez-Ackerman, Pérez, & Tremblay, 2011). Generally, recruitment and establishment are water limited, particularly in epiphytes in their early life stages because they have no water storage organs. Previous studies on this system show that abundance of seedling decreases with increasing number of dry days (Olaya-Arenas et al., 2011). Therefore, increasing temperatures may reduce seedling establishment due to increasing transpiration resulting in dryer conditions and desiccation.

The negative effects of increasing minimum temperature or variability in maximum temperature were less severe in patches containing larger areas of moss. Previous studies show that moss facilitates the establishment of *Lepanthes* in trees and rock phorophytes (García-Cancel et al., 2013) and distribution around the bole

of the tree (Tremblay & Castro, 2009). A similar pattern has been found in the epiphytic lichen *Lobaria pulmonaria* where host tree diameter is positively related to colonization (Snäll, Pennanen, Kivistö, & Hanski, 2005). One potential mechanism behind increasing colonization rates with increasing moss area but decreasing minimum temperatures is that moss may help mitigate the potential negative effects of increasing temperature by providing required moist to ensure propagule establishment (Bulleri, Bruno, Silliman, & Stachowicz, 2016). However, when temperature increases beyond the thermal tolerance for both species (host and orchid), it may cause stress on both and shift the relationship from facilitation by the host moss to competition between the host and the orchid for water resources (Olsen, Töpfer, Skarpaas, Vandvik, & Klanderud, 2016). A shift in the outcome of biotic interactions due to climate change is an interesting follow-up hypothesis to test.

Our results demonstrate that variability in maximum temperature both decreases local colonization and increases local extinction, which is noteworthy because the role of climate variability on ecological and evolutionary processes is understudied (Vázquez, Gianoli, Morris, & Bozinovic, 2017). The effects of climate variability emphasize the interplay between weather extremes and plant thermal optima. Temperature variability may also influence colonization and extinction dynamics by affecting phenological and physiological processes that result in a decrease in establishment and an increase in within-patch mortality (Reyer et al., 2013). Lastly, increasing climatic variability may influence colonization and extinction dynamics indirectly by affecting community-level processes. For example, variability in maximum temperature may change phenological dynamics of pollinators that may ultimately decrease *Lepanthes* recruitment. Although we know little about the potential pollinators of this species, they are likely ectothermic insects whose physiological and demographic processes are particularly sensitive to variation in temperature (Memmott, Craze, Waser, & Price, 2007). Therefore, while our results emphasize the role of climatic variability for local colonization–extinction dynamics, there is a need for further research on the ecological and evolutionary mechanisms by which climate variability influences populations (Vázquez et al., 2017).

Will the study population persist, shift or decline towards extinction? Our results showing a decrease in equilibrium occupancy and overall extinction in smaller patches provides little support for the hypothesis that this *Lepanthes* population will be able to persist under future climate predictions. The potential for adaptation to increasing temperatures is also low. The genus *Lepanthes* (>1,100 species: Crain & Tremblay, 2014) is known to have population structures with small populations (Tremblay, 1997), small effective population sizes, infrequent pollination events (Tremblay, 2000; Tremblay & Ackerman, 2001) and limited gene flow even among close by demes (Tremblay & Ackerman, 2001), which are all indicators that genetic drift may be common. In addition, evidence of phenotypic selection in *L. rupestris* is present within/demes populations, however, inconsistent among time and space and the type of selection (Cintrón-Berdecía & Tremblay, 2003; Tremblay, 2011). However, the ability of *L. rupestris* to adapt to varying climate conditions cannot be discounted if the diversity of

habitat where other species of *Lepanthes* are found is an indication of adaptation potential. Nevertheless, adaptation through natural selection would likely occur at a longer time-scale than the expected climatic changes.

Range shifts appear to be an unlikely alternative for *L. rupestris* to cope with climate change. We found that elevation was not an important predictor of colonization or extinction which gives little evidence that shifts are occurring. Furthermore, the species is highly dispersal limited (4.8 m average dispersal distance) with less than one successful migrant per generation (Tremblay, 1997). While *L. rupestris* may have more favourable conditions for persistence upstream where temperatures are lower (Waide et al., 2013), wind patterns favour dispersal in the opposite direction (Figure 1). Therefore, the disequilibrium between colonization and extinction favouring extinction may not be counterbalanced by adaptation or shift, which leads to an overall decline as the most plausible future scenario. Our results are consistent with model projections that predict that dispersal-limited organisms have 250% higher likelihood of going extinct under climate change (Thomas et al., 2004). Higher risk of extinction for dispersal-limited organisms is also supported by microcosm experiments that show that systems that experience dispersal asymmetries have lower tolerance for challenging environments (Limdi, Pérez-Escudero, Li, & Gore, 2018). Therefore, extinction risk may be higher for asymmetric dispersers that are unable to persist under climate change scenarios because their potential for shifts is spatially limited (Sorte, 2013). Overall, our results suggest that asymmetrically dispersed epiphytes will struggle to keep up with climate change because connectivity will not be strong enough to counterbalance the potential negative effects of climate change.

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AUTHORS' CONTRIBUTIONS

M.A.A. and L.B. designed the study; R.L.T. and E.J.M.-A. collected the data; M.A.A. analysed the data; M.A.A. wrote the manuscript with contributions from all authors.

DATA AVAILABILITY STATEMENT

The data used in this study are available in Dryad Digital Repository: <https://doi.org/10.5061/dryad.9p8cz8wc6> (Acevedo, Beaudrot, Meléndez-Ackerman, & Tremblay, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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