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POPULATION ECOLOGY - ORIGINAL RESEARCH

Spatial asymmetries in connectivity influence colonization−extinction dynamics

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Abstract Movement has broad implications for many areas of biology, including evolution, community and population ecology. Movement is crucial in metapopulation ecology because it facilitates colonization and reduces the likelihood of local extinction via rescue effects. Most metapopulation modeling approaches describe connectivity using pair-wise Euclidean distances resulting in the simplifying assumption of a symmetric connectivity pattern. Yet, assuming symmetric connectivity when populations show net asymmetric movement patterns may result in biased estimates of colonization and extinction, and may alter interpretations of the dynamics and conclusions regarding the viability of metapopulations. Here, we use a 10-year time series on a wind-dispersed orchid *Lepanthes* *rupestris* that anchors its roots in patches of moss growing on trees or boulders along streams, to test for the role of connectivity asymmetries in explaining the colonization−extinction dynamics of this orchid in a network of 975 patches. We expected that wind direction could highly alter dispersal direction in this orchid. To account for this potential asymmetry, we modified the connectivity measure traditionally used in metapopulation models to allow for asymmetric effective distances between patches and subsequently estimated colonization and extinction probabilities using a dynamic occupancy modeling approach. Asymmetric movement was prevalent in the *L. rupestris* metapopulation and incorporating potential dispersal asymmetries resulted in higher colonization estimates in larger patches and more accurate models. Accounting for dispersal asymmetries may reveal connectivity effects where they were previously assumed to be negligible and may provide more reliable conclusions regarding the role of connectivity in patch dynamics.

Keywords Asymmetric dispersal · *Lepanthes* · Metapopulation · Target effects · Movement

Communicated by John Thomas Lill.

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Introduction

Variation in movement has broad implications for evolutionary biology (Kawecki and Holt 2002), community ecology (e.g., Tilman et al. 1994; Salomon et al. 2010), and population dynamics (Armsworth and Roughgarden 2005). In metapopulation ecology, movement is a fundamental process influencing metapopulation dynamics and local population persistence over time (Hanski 1998). Often, the focus on movement emphasizes dispersal from natal environments or previous breeding locations (Clobert et al.

2001). Here, we broadly use the term "dispersal" to reflect movements that generate variation in emigration, immigration, and colonization rates (sensu Vuilleumier et al. 2010).

Most metapopulation approaches describe colonization−extinction dynamics following the area-isolation paradigm (Hanski 1998; Pellet et al. 2007). Under this paradigm, extinction is negatively related to patch area [assuming that population size increases with patch area (Hanski 1999)], and colonization is negatively related to isolation from other patches. Patch isolation is often quantified using connectivity measures (inverse of isolation) that assume the probability of colonization declines with increasing distance to surrounding occupied patches, which act as sources of propagules. To do so, these measures typically use a dispersal kernel weighted by the occupancy state and area of surrounding patches (Moilanen and Nieminen 2002).

While these connectivity metrics have proven useful, dispersal kernels make assumptions regarding the movement behavior of the species and how the environment influences movement. For instance, a negative exponential function based on Euclidean distance is commonly assumed in many patch connectivity measures (Hanski 1998; Moilanen and Nieminen 2002). Assuming a kernel based on Euclidean distance results in the implicit assumption of symmetric dispersal in which the likelihood of dispersal from patch i to patch j is the same as the likelihood of dispersal from patch j to i. Nevertheless, several factors in nature often cause an asymmetric pattern of dispersal, such as spatial heterogeneity in landscape features (e.g., Ferreras 2001; Prevedello and Viera 2010) and advection sources [e.g., wind, ocean and marine currents (Treml et al. 2008)].

An asymmetric pattern of dispersal may arise due to variations in patch or inter-patch attributes. At the patch scale, variation in patch area may result in a greater likelihood of dispersal towards large patches because active dispersers may better detect these or because these are large targets for passive dispersers [i.e., target effects (Gilpin and Diamond 1976; Lomolino 1990)]. Quantitatively, these asymmetries due to patch-scale variation have been traditionally incorporated in connectivity measures by weighting a dispersal kernel by patch area. Inter-patch attributes, such as advection sources (e.g., wind, ocean or river currents), may result in a greater likelihood of dispersal in the direction of the advection source than in the opposite direction (e.g., Treml et al. 2008). That is, the effective distance in the direction of the advection source may be less than the effective distance in the opposite direction.

Connectivity measures currently used in metapopulation modeling generally lack a formal way to incorporate this kind of asymmetry in effective distance. Moilanen and Hanski (1998) provide ways to account for habitat

type-specific effective distances; however, in these models the effective distance measure is still assumed to be symmetric. Other alternate parameterizations employ least-cost paths (LCP) between patches (Chardon et al. 2003). Even though they have been shown to be better descriptors of effective distance than Euclidean distance (e.g., Sawyer et al. 2011), in most applications these LCPs are also symmetric ($LCP_{ij} = LCP_{ji}$).

Recent metapopulation theory hypothesizes that failing to acknowledge dispersal asymmetries may lead to biased patch connectivity estimates, which in turn affect estimations of colonization and extinction dynamics, leading to incorrect assessments of the interpretations of the future viability of metapopulations (Vuilleumier and Possingham 2006; Bode et al. 2008; Vuilleumier et al. 2010). Yet there are very few empirical tests of these hypotheses, in part because we lack an adequate way to quantitatively incorporate asymmetric inter-patch attributes in metapopulation models (but see Vuilleumier and Fontanillas 2007).

Here, we use a long-term, time series on colonization−extinction dynamics in the wind-dispersed orchid *Lepanthes rupestris* to test for asymmetric dispersal. We assess the role of asymmetries for colonization and extinction dynamics by extending the connectivity function of Hanski (1994) to account for dispersal asymmetry due to wind advection. We expected asymmetric dispersal would be prevalent in this metapopulation and that such asymmetries would alter colonization and extinction estimates relative to models assuming dispersal symmetries.

Materials and methods

Study system

Orchids, such as *Lepanthes rupestris*, that grow on rock (epilithic) and/or trees (epiphytic) are appropriate for investigating asymmetric dispersal in a metapopulation context, because they often live in spatially discrete, ephemeral habitats and are passively dispersed by directed sources such as wind (e.g., Tremblay et al. 2006). Moreover, many epiphytic and epilithic orchids are subject to colonization and extinction dynamics due to their small population sizes and stochastic reproductive success driven, in part, by dispersal and pollinator limitation (Ackerman 1995; Tremblay 1997; Tremblay and Ackerman 2001, 2003; Olaya-Arenas et al. 2011).

L. rupestris is a small, wind-dispersed orchid (leaves 1.3−4.3 cm, shoots 15 cm in height and flowers of <6 mm) commonly found along the riverbeds of the Luquillo Mountains in Puerto Rico (Ackerman 1995). This patchily distributed orchid anchors its roots to the substrate and roots are often covered by moss living on the surfaces of

trees or rocky boulders (phorophytes). On average rocks have larger population sizes and higher occupancy rates than trees (Tremblay et al. 2006). This orchid's life span is highly variable with an average of 3.4 years (Tremblay 2000). The seeds are microscopic with a mean dispersal distance of 4.8 m (Tremblay 1997). Given the small size of the seeds, little is known about their fate after dispersal, and the presence of seed banks in orchids in general has been debated. Whigham et al. (2006) found that temperate orchid seeds in experimental conditions were viable after 7 years; however, field experiments on the viability of the terrestrial orchids *Caladenia arenicola* and *Pterostylis sanguinea* showed that seed viability declines rapidly in less than a year, following the onset of the wet season (Batty et al. 2000). Similarly, *Lepanthes* seeds are expected to die if they fall in the river (Tremblay et al. 2006); therefore, given the flood dynamics of tropical rivers (Johnson et al. 1998), the effect of seed banks in the metapopulation dynamics of this orchid are likely negligible.

A permanent plot for the study of the metapopulation dynamics of *L. rupestris* was established in Quebrada Sonadora in the Luquillo Experimental Forest (18°18′N, 65°47′W) in 1999. This permanent plot is composed of 1000 occupied and unoccupied boulders and tree trunks ("patches" hereafter) (Tremblay et al. 2006). Initially, a total of 250 occupied patches (165 boulders and 85 trees) were identified. A patch was considered occupied if at least one living individual was present. Unoccupied patches were identified by randomly selecting three suitable patches (of any phorophyte with moss cover) with no individuals of any stage inside a 5-m radius of an initially occupied patch

(Tremblay et al. 2006). Around 57 % of these 750 patches remained unoccupied for the length of the study. These patches are spatially configured as an almost linear array following the river topography in a steep elevation gradient (Fig. 1). Most patches (975) were mapped to within approximately 10 cm (*x*, *y*, *z* position) relative to the center of each patch using metal rulers, a sighting compass and a clinometer (Fig. 1). The presence/absence of *L. rupestris* was surveyed twice a year from 1999 to 2008 (at the beginning of the year and in the summer), with the exception of 1999, 2006 and 2008 that were surveyed once. Because these orchids depend on moss living in rock or tree phorophytes to anchor their roots, patch size was estimated as the total moss area in the phorophyte, measured using a 150-cm^2 grid.

Average wind direction was calculated from hourly measures taken by the nearest weather station located in El Verde Biological Station (Ramírez and Melendez-Colom 2003), <300 m from the study site. Wind direction was variable (Online Resource 1) and on average followed the direction of the river. Dispersal of *L. rupestris* is thought to be restricted to trees and boulders in the river because the forest surrounding the river limits the amount of wind that could potentially disperse the orchid beyond the river's edge (R. L. Tremblay, personal observation). We calculated average wind direction for each year from measures taken between primary periods (i.e., measures taken between the last survey of the current year and the first survey of the next; see below). Wind data were available for most of the sampling periods (2001−2004 and 2006−2008). Each of these sampling periods was characterized by its

Fig. 1 Map showing **a** the spatial arrangements of local populations of *Lepanthes rupestris* in rock and tree phorophytes located in Quebrada Sonadora, a first-order tributary of the Espíritu Santo River in the Luquillo Experimental Forest (US Department of Agriculture Forest Service). We used occupancy data collected from 1999 to 2008 to compare model fit and colonization−extinction estimates of occupancy models incorporating a connectivity measure that assumed **b** symmetric effective distances and **c** estimates of the asymmetric effective distances of seed dispersed due to wind advection. *Black circles* represent rock phorophytes, *gray circles* represent tree phorophytes
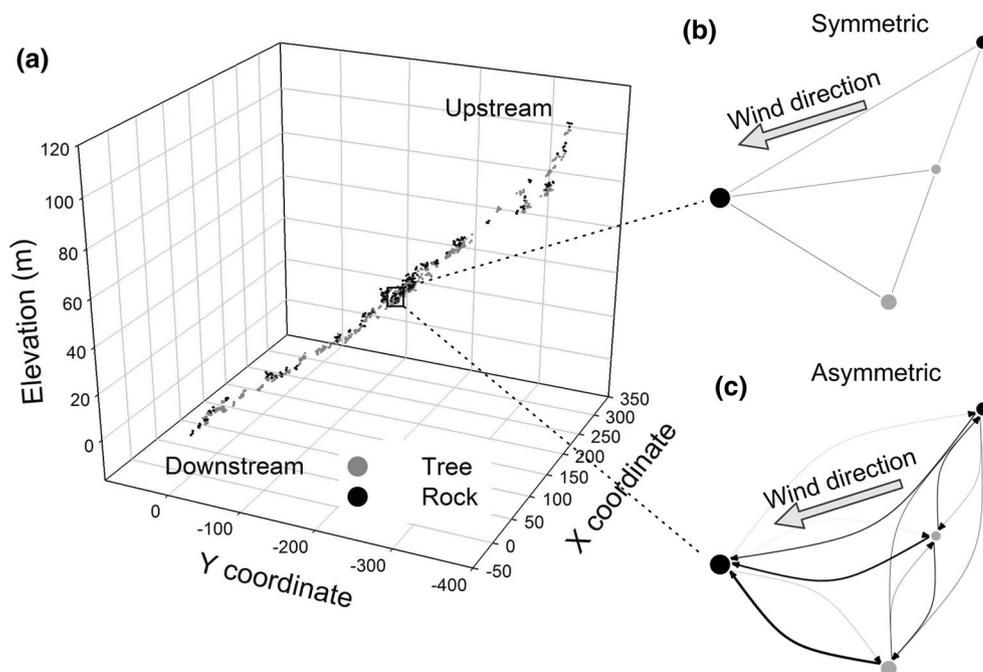
year-specific average wind direction. Wind data were unavailable for 1999, 2000 and 2005; hence, we used the average value of all sampling periods to represent wind direction in these missing years. We also analyzed the data using wind direction weighted by maximum wind speeds and obtained the same qualitative results.

Site occupancy model and parameter estimation

Incidence function models (IFM) (Hanski 1999; Moilanen 2002) are arguably the most common modeling approaches used to understand colonization and extinction dynamics in a metapopulation context. IFMs assume that a species lives in a network of patches surrounded by an inhospitable matrix. In our system, the inhospitable matrix is the stream surrounding the trees and boulder phorophytes because the seeds that fall in the water are not viable. Our system meets the inhospitable matrix assumption, yet, IFMs make other two assumptions that are difficult to meet in many applications. First, they assume that the species is always detected where it is present (i.e., perfect detection). This is rarely the case, where an observed absence may be either a true absence (the population is locally extinct) or simply that the species was not detected, which may result in an overestimation of extinction (Moilanen 2002). Second, IFMs assume that metapopulations are at a Markovian pseudo-equilibrium in which the occupancy status of each patch at time t is given only by the patch status at time $t - 1$. This assumption is difficult to test and some studies argue that it is more appropriate to assume nothing about the equilibrium state of the metapopulation (Moilanen 1999; Pellet et al. 2007). In this study, we applied an alternate method, a dynamic occupancy model, in which these two assumptions are relaxed (MacKenzie et al. 2003).

The dynamic (multiple-season) occupancy modeling approach resembles Pollock's robust design (Pollock 1982) in that there are two types of sampling periods. Primary periods are used to estimate colonization and extinction parameters. The population is assumed to be open between these primary periods. During the primary periods, sites are surveyed multiple times (secondary sampling). The population is assumed to be closed (no immigration, emigration, births, or deaths) between these secondary sampling periods (see Rota et al. 2009), which are used to estimate detection probabilities. For each secondary sampling period, there are three occupancy possibilities: presence, absence (which may correspond to imperfect detection or an actual absence), or missing data (MacKenzie et al. 2003).

Our primary sampling periods are years (1999−2008, $n = 10$). The secondary sampling periods consisted of two censuses that were performed within each year. One census was conducted at the beginning of the year (between January and February) and the second in the summer (between

July and August). This model formulation allows the system to be open to colonizations and extinctions during the wet season. Tropical storms are common during the wet season causing flash floods, which may be responsible for most local extinctions and anomalous strong winds, which may increase the magnitude of dispersal events potentially resulting in more local colonizations (Tremblay et al. 2006).

Even though some colonizations and extinctions may happen in the dry season these are likely to be minimal given the high detectability estimates (see "Results"). Given the small size of the orchid, we expected variation in detectability especially in patches with small areas of moss where it may be difficult to discern between moss and a small individual of *L. rupestris*.

The effects of patch area (A_i) and patch connectivity (S_i) of focal patch i were added as site covariates to model colonization and extinction. A_i was also added as a site covariate for detection probabilities. We calculated S_i in two ways; the first treats the distance effect in the dispersal kernel as symmetric and the second adjusts effective distance to allow for asymmetric movement. S_i with a symmetric dispersal kernel was calculated using the general approach applied in many IFM (Moilanen and Nieminen 2002):

$$S_{i,t}^{\text{sym}} = \sum_{j \neq i}^{N} \exp(-\alpha d_{ij}) p_{j,t} A_j, \tag{1}$$

where N is the total number of patches in the landscape, $1/\alpha$ is the average dispersal distance of the species, d_{ij} is the Euclidean distance between patches i and j, and A_j is the area of patch j (Hanski 1998, 1999). Note that we use focal A_i as a site covariate and patch area of potential sources (A_j) as part of the connectivity function. Therefore, patch area is contributing different information when used in the connectivity measure and as a site covariate. In this case, $p_{j,t}$ represents the naïve binary occupancy state of patch j in year t, that restricts patch connectivity to only occupied sites. This naïve estimate assumes perfect detection. We found detection probabilities to be very high ($p > 0.85$; Online Resource 2); hence, we used these occupancy states as an approximation for the connectivity measure (cf. Royle and Dorazio 2008). Nevertheless, we explicitly estimated detection probability when estimating colonization and extinctions (see below). Note that the effective distance between patches in this model is symmetric (i.e., $d_{ij} = d_{ji}$). This formulation can result in asymmetric patch connectivity due to variation in patch area, but not due to variations in effective distance among patches (i.e., inter-patch attributes).

We modified Eq. 1 to incorporate the effect of average wind direction each year in the estimation of connectivity. Patch connectivity with an asymmetric dispersal kernel was calculated as:

$$S_{i,t}^{\text{asym}} = \sum_{j \neq i}^{N} \exp\left(-\alpha \frac{d_{ij}}{1 - \delta_{ij,t}}\right) p_{j,t} A_j, \qquad (2)$$

where $\delta_{ij,t}$ describes the difference between the angle of wind direction in year t and the angle between patches i and j in radians with respect to the horizontal axis (Fig. 2). This modeling approach resembles the strongly asymmetric distance-dependent model of Vuilleumier et al. (2010) in which δ is incorporated as a modifier inside the exponential decay function. For simplicity, $\delta_{ij,t}$ is scaled by π to constrain $\delta_{ij,t} \in [0, 1)$, such that,

$$\delta_{ij,t} = \frac{|\theta_{ij} - \theta_{\text{wind},t}|}{\pi}, \qquad (3)$$

where θ_{ij} represents the angle between patches i and j with respect to the horizontal axis and $\theta_{\text{wind},t}$ represents the average angle of wind direction in year t. For both measures of patch connectivity (S_{sym} and S_{asym}), connectivity decreases with increasing distance between patches. In S_{asym} when $\delta_{ij,t} = 0$, the effective distance between patches is the same as Euclidean distance, and hence $S_{\text{asym}} = S_{\text{sym}}$; however, as $\delta_{ij,t}$ increases, the effective distance between patches increases, resulting in decreased connectivity when compared to S_{sym}. This modification allows an asymmetric dispersal kernel because the effective distance between patches in the direction of wind is less than the effective distance between the same patches in the opposite direction (against wind direction).

The distribution of the δ parameter will depend on the spatial arrangement of the patches with respect to the angle of the advection source. For instance, if patches are
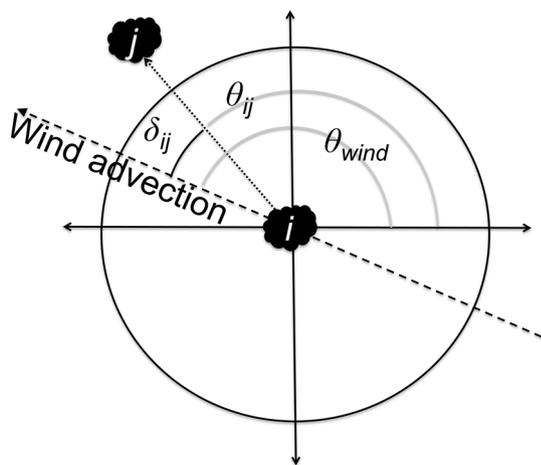
Fig. 2 Diagram showing how δ_{ij}, calculated as the difference of the angles between patches i and j, and the angle of wind direction with respect to the horizontal axis (easting), is used to assess the magnitude of dispersal asymmetry due to wind advection. θ_{ij} represents the angle between patches i and j with respect to the horizontal axis, and θ_{wind} represents the average angle of wind direction

randomly arranged in space, we will expect a uniform distribution of δs (Online Resource 3). In contrast, if patches are spatially aligned parallel to the angle of the advection source (e.g., along a river when wind advection is going downstream), we will expect a bimodal distribution (Online Resource 3). The bimodal nature of the distribution is expected because the difference in the angles was scaled by π, and thus $\delta_{ij} + \delta_{ji} = 1$. As the difference between $\delta_{ij,t}$ and $\delta_{ji,t}$ increases, effective distance becomes more asymmetric, and the distribution will become more skewed towards the limits of the distribution.

We fitted the following kinds of dynamic occupancy models. Each model type represented a hypothesis explaining the underlying mechanism governing colonization and extinctions in the *L. rupestris* metapopulation. Traditionally, patch occupancy models in a metapopulation context originate from the area-isolation paradigm, where patch area influences extinction rates and isolation influences colonization rates. Hence:

1. The "area-isolation" model includes patch connectivity as a site covariate for colonization and patch area as a site covariate for extinction [i.e., $\gamma(S)$, $\varepsilon(A)$, where γ represents colonization, ε extinction, S represents a measure of connectivity either with a symmetric or asymmetric dispersal kernel, and A describes patch area of focal patch i]. Connectivity may also decrease extinction probability by the rescue effect of nearby patches (e.g., Hanski 1998).

2. The "rescue effects" model includes connectivity as a site covariate for colonization, and both connectivity and patch area as site covariates for extinction i.e., $\gamma(S)$, $\varepsilon(S + A)$. Given the wind-dispersed nature of *L. rupestris*, we expect that larger patches may have a greater likelihood of receiving seeds because they are larger targets.

3. Hence, we also fitted a "target effects" model in which patch connectivity together with patch area are incorporated as covariates for colonization and patch area as a covariate for extinction, i.e., $\gamma(S + A)$, $\varepsilon(A)$.

4. We also fitted a "target-rescue effects" model, which included both target and rescue effects i.e., $\gamma(S + A)$, $\varepsilon(S + A)$.

   For each of these models (1−4) we contrasted a model with S_{sym} and another with S_{asym} as a site covariate.

5. Because connectivity may not necessarily be an important factor predicting colonization and extinction dynamics (Pellet et al. 2007), we also fitted a model that had moss area as site covariate for colonization and extinction, but no connectivity.

Previous analyses for this species have found that colonization and extinction dynamics may be different depending on phorophyte type [tree or rocky boulder (Tremblay et al. 2006)]. Therefore, phorophyte type of the focal patch i was also tested as a predictor of colonization and extinction in these five model types. Also, for each of these five models we tested for the effects of phorophyte type, and patch area as important site covariates for detectability.

6. Finally, we also fitted a null (intercept-only) model with no covariates to compare with more complex models.

We ranked each occupancy model based on its Akaike information criterion (AIC) (Burham and Anderson 2002). Models with the lowest AIC were considered most parsimonious. We fitted each model using maximum likelihood with covariates scaled and centered. Occupancy models were fitted using the package unmarked (Fiske and Chandler 2011) in R.

We combined the estimated colonization (γ) and extinction (ε) parameters to estimate equilibrium patch occupancy ψ^*,

$$\psi^* = \frac{\gamma}{\gamma + \varepsilon}. \tag{4}$$

This equilibrium occupancy describes the proportion of patches expected to be occupied if the colonization and extinction rates remain constant in the long term (Ferraz et al. 2007). We used this measure to compare predicted equilibrium occupancy for the most parsimonious model (which included asymmetric connectivity as a covariate for colonization, see below) and its analogous model that incorporates symmetric connectivity as site covariate for colonization.

Results

The average Euclidean distance between patches was 125.51 m $\pm$ 3.10 SE. Average patch area (i.e., total moss area) in rock phorophytes was 55.6 cm^2 $\pm$ 3.38 SE, which were on average slightly larger than tree phorophytes (38.90 $\pm$ 2.38; Online Resource 4). The percentage of observed occupied patches in primary periods ranged from 22 to 27 % (Fig. 3). Average wind direction ranged from 1.14 to 2.40 rad with an average for all sampling periods of 2.15 rad (Online Resource 1). The calculated values for δ ranged between 1.11×10^{-6} and 9.9×10^{-1}. The distribution of the δ_{ij} showed a bimodal distribution, skewed towards the limits of the distribution (Online Resource 5).
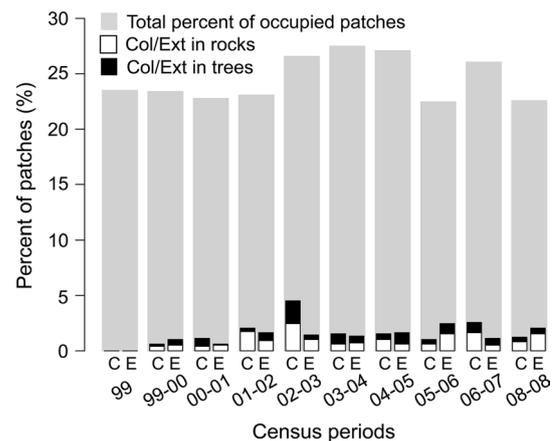
Fig. 3 Summary of observed percent of patches occupied each year, and observed colonizations (*Col*) and extinctions (*Ext*) of local populations of *L. rupestris* over census primary periods. These observed colonization and extinctions are naïve estimates because they assume perfect detection; however, estimated colonization and extinctions incorporated detection probability was very high ($p > 0.85$)

Based on dynamic occupancy models, detection probability was generally high ($p > 0.85$) and positively related with patch area in both phorophytes (Online Resource 2).

The target and target-rescue effects models had better fit than the no connectivity model suggesting that patch connectivity is an important predictor of patch dynamics in this system, with the target effects model being most parsimonious. This model included patch area and patch connectivity with an asymmetric dispersal kernel (S_{asym}) as site covariates for colonization ("asymmetric model" hereafter). This model predicted the odds of a patch being colonized to be on average 1.43 ($\pm$0.13 SE) for a unit increase in asymmetric connectivity and 1.67 ($\pm$0.12 SE) for a unit increase in moss area (Online Resource 6). This asymmetric model predicted equilibrium occupancy for tree phorophyte to be $\psi^*_{asym(TREE)} = 0.73$ and $\psi^*_{asym(ROCK)} = 0.58$ for the rock phorophyte. This asymmetric model had more support than the similar model (target effects model) that included the patch connectivity measure with a symmetric dispersal kernel as a site covariate (S_{sym}; "symmetric model" hereafter; Table 1). This symmetric model predicted the odds of a patch being colonized to be on average 1.31 ($\pm$0.14 SE) for a unit increase in symmetric connectivity and 1.65 ($\pm$0.12 SE) for a unit increase in moss area, for fixed values of patch area and phorophyte type (Online Resource 7). This symmetric model predicted equilibrium occupancy for tree phorophyte to be $\psi^*_{asym(TREE)} = 0.71$ and $\psi^*_{asym(ROCK)} = 0.55$ for the rock phorophyte. Therefore, the asymmetric (most parsimonious) model predicted on average higher colonization rates than the symmetric model, specially for larger phorophytes (Figs. 4, 5) and slightly higher equilibrium occupancy. In all five model types, the

Table 1 Comparison of model fit for dynamic occupancy models using symmetric (S_{sym}) and asymmetric (S_{asym}) connectivity measures, phorophyte type (Ph) and patch area (A) as site covariates

Hypothesis	Model	ΔAIC	AIC	Parameters	AIC$_{weight}$
Asymmetric: target	$\psi(.), \gamma(S_{asym} + A + Ph), \varepsilon(A), p(A + Ph)$	0	4321.65	10	0.43
Asymmetric: target-rescue	$\psi(.), \gamma(S_{asym} + A + Ph), \varepsilon(S_{asym} + A), p(A + Ph)$	1.81	4323.46	11	0.17
Symmetric: target	$\psi(.), \gamma(S_{sym} + A + Ph), \varepsilon(A), p(A + Ph)$	6.04	4327.69	10	0.02
Symmetric: target-rescue	$\psi(.), \gamma(S_{sym} + A + Ph), \varepsilon(S_{sym} + A), p(A + Ph)$	8.04	4329.69	11	<0.01
No connectivity	$\psi(.), \gamma(A + Ph), \varepsilon(A + Ph), p(A + Ph)$	11.39	4333.04	10	<0.01
Asymmetric: area-isolation	$\psi(.), \gamma(S_{asym} + Ph), \varepsilon(A), p(A + Ph)$	22.8	4344.45	9	<0.01
Asymmetric: rescue	$\psi(.), \gamma(S_{asym} + Ph), \varepsilon(S_{asym} + A + Ph), p(A + Ph)$	26.04	4347.69	11	<0.01
Symmetric: area-isolation	$\psi(.), \gamma(S_{sym} + Ph), \varepsilon(A), p(A + Ph)$	27.48	4349.13	9	<0.01
Symmetric: rescue	$\psi(.), \gamma(S_{sym} + Ph), \varepsilon(S_{sym} + A + Ph), p(A + Ph)$	29.48	4351.12	10	<0.01
Null	$\psi(.), \gamma(.), \varepsilon(.), p(.)$	96.52	4418.17	4	<0.01

For clarity we show only the best model for each hypothesis explaining the colonization and extinction of *L. rupestris*. See Online Resource 8 for the complete analysis results

AIC Akaike information criterion, ψ occupancy, γ colonization, ε extinction, p detection
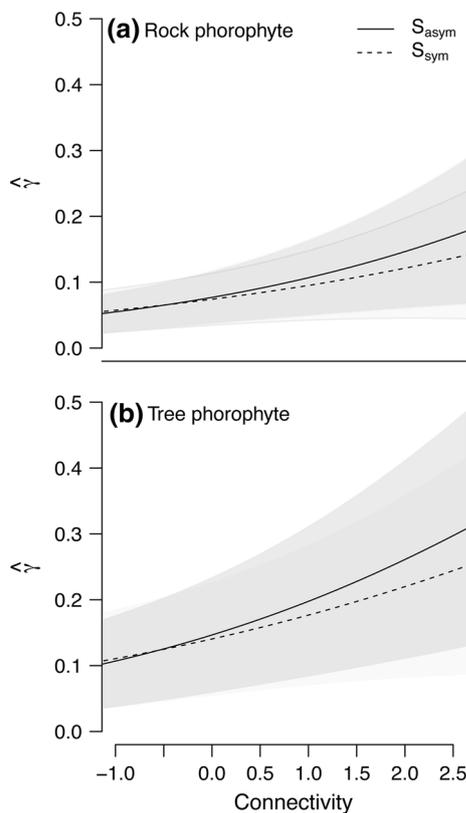
Fig. 4 Partial relationships between colonization and connectivity measures [symmetric (S_{sym}) and asymmetric (S_{asym})] taken from the best-fit model, $\Upsilon(S_{asym} + A + Ph), \varepsilon(A + Ph)$, where γ is colonization, A is patch area, Ph is phorophyte type and ε is extinction, and its symmetric analog, $\Upsilon(S_{sym} + A + Ph), \varepsilon(A + Ph)$ for the **a** rock and **b** tree phorophytes. *Shaded areas* represent 95 % confidence interval for each of the connectivity measures. Note that the range of the connectivity axis represent the values of S_{sym} and S_{asym} scaled and centered
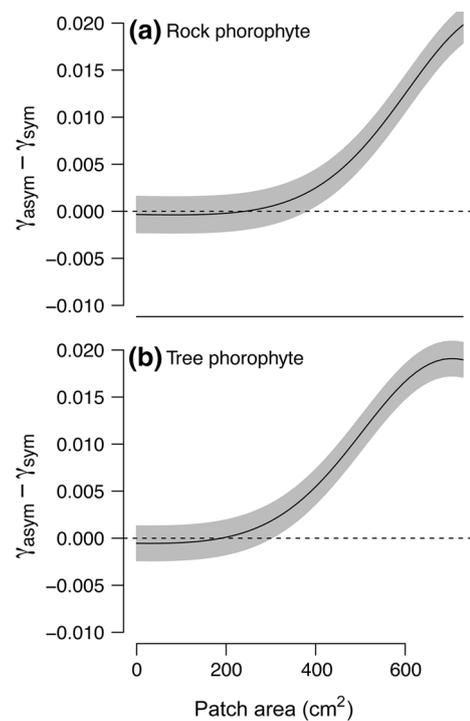
Fig. 5 Difference between colonization estimates among the best-fit model, $\psi(.), \gamma(S_{asym} + A + Ph), \varepsilon(A + Ph), p(A + Ph)$, where ψ is occupancy, and its symmetric analog, $\psi(.), \gamma(S_{sym} + A + Ph), \varepsilon(A + Ph), p(A + Ph)$ for **a** rock and **b** tree phorophytes. This difference ($\gamma_{asym} - \gamma_{sym}$) increases exponentially with patch area. This partial relationship is shown for average connectivity (S). *Shaded areas* show bootstrapped 95 % confidence intervals. For other abbreviations, see Fig. 4

asymmetric form of the model had more support based on AIC than the corresponding symmetric model (Table 1; see Online Resource 8 for the full table of model comparisons).

Both models (asymmetric and symmetric) predicted a similar positive relationship between increasing patch area and colonization (Online Resources 6, 7). There was little difference between the colonization probabilities predicted by both models for small patches; however, the asymmetric model predicted higher colonization rates for larger patches (Fig. 5). Colonization was 2.06 ($\pm$0.53 SE) times as likely for tree phorophytes as for boulder phorophytes in both models (Online Resources 6, 7; Fig. 5).

Discussion

Most metapopulation models assume symmetric effective distances between patches. These symmetries may be uncommon in nature where organisms move through heterogeneous landscapes (Gustafson and Gardner 1996). Here we developed a novel modification of the connectivity formulation traditionally used in IFM that allows for asymmetric effective distances between patches when dispersal is directed by an advection source. Our results on the wind-dispersed orchid *Lepanthes rupestris* suggest that asymmetric dispersal was prevalent in this system and that its colonization−extinction dynamics were better described by a metapopulation model that incorporated this modified asymmetric connectivity formulation. This approach expands on previous analysis, which showed that colonization rates in *L. rupestris* were not well predicted by symmetric exponential and ring models, while extinction probabilities were (Kindlmann et al. 2014).

Our results suggest the potential of target effects as an important mechanism predicting colonizations (Gilpin and Diamond 1976; Brown and Kodric-Brown 1977; Lomolino 1990; Online Resource 9). Moreover, the implications of asymmetric dispersal were greater for larger patches, because the asymmetric model better described the process by which large patches are more likely to receive wind-dispersed propagules. Yet, the difference in predicted colonization probability between the asymmetric and symmetric models for large patches was moderate, possibly due to the relative low frequency of large patches in the system (only 22 patches were larger than 250 cm^2; Online Resource 4). Similar relationships between connectivity and patch size predicting colonization have been reported for other epiphytic species. For instance, tree diameter and connectivity have been positively related to colonization in the epiphytic lichen *Lobaria pulmonaria* (Snäll et al. 2005) and the epiphytic bryophytes *Nyholmiella obtusifolia*, *Orthortichum speciosum*, *Pylaisia polyantha,* and *Radula complanata* (Hazell et al. 1998). Also, similar positive relationships between patch size and colonization rates have been described in active dispersers, such as the butterfly *Maculinea nausithous* (Hovestadt

et al. 2011) and the migratory bird *Empidonax minimus* (Fletcher 2009).

Other factors might also affect the colonization and extinction dynamics of *L. rupestris* in addition to connectivity, patch area and phorophyte type. For instance, seed establishment in orchids is limited by their association with mycorrhizae (Rasmussen and Whigham 1993; McCormick et al. 2012; McCormick and Jacquemyn 2013). The thickness of moss layers might influence the probability of seedling establishment. Since seedlings are more abundant in patches where the moss layer is thinner (García-Cancel et al. 2014). Also, the amount of moss moisture may also affect seed establishment (Tremblay et al. 2006). These variables were not included in this model due to the difficulty of incorporating these into a long-term metapopulation monitoring program. Their potential interaction with asymmetric connectivity to predict colonization and extinction dynamics remains unexplored and should be considered in future efforts.

We found that connectivity was important to predict colonizations and extinctions, and that asymmetric dispersal is prevalent in the system. A previous analysis on ten species of birds, amphibians and butterflies showed that adding connectivity as a site covariate did not improve model fit compared to constant colonization parameters (Pellet et al. 2007). Pellet et al. (2007) argued that using a symmetric connectivity measure, as is traditionally used in IFM, may not be adequate to model most species because it does not account for density-independent movements among patches (e.g., response to an advection source or taxis), which may significantly affect dispersal rates. The S_{asym} connectivity measure in this study accounts for some of these density-independent movements.

There is some debate in the theoretical literature about the implications of asymmetric dispersal for metapopulation dynamics. Some studies argue that asymmetric dispersal decreases connectivity, resulting in increasing extinction risk and lower metapopulation viability (Vuilleumier and Possingham 2006; Bode et al. 2008; Vuilleumier et al. 2010). In contrast, Kleinhans and Jonsson (2011) found less negative consequences of asymmetric dispersal for metapopulation viability when controlling for the density of dispersal connections. They argue that the magnitude of the implications of asymmetric dispersal for metapopulation dynamics is likely to be moderate when considering asymmetric dispersal in conjunction with other factors relevant to metapopulation viability. Our results show some support for this idea. We found that the asymmetric model better described the colonization−extinction dynamics of *L. rupestris*, but the difference between colonization, extinction and equilibrium occupancy between the asymmetric and symmetric models was moderate, most likely because we considered asymmetric dispersal in conjunction with other

factors. Patch area and phorophyte type had similar effect sizes and also play an important role driving the metapopulation dynamics of this orchid.

There are several examples of organisms, including both active and passive dispersers, that live in metapopulations with asymmetric connectivity. For instance, the closely related species *Lepanthes eltoroensis*, exhibited directionality in successfully colonized trees (Tremblay and Castro 2009). In aquatic systems, ocean and river currents are important drivers of asymmetric dispersal for both vertebrates and invertebrates (e.g., Treml et al. 2008). Asymmetric dispersal patterns have also been found in active dispersers such as Everglade snail kites (*Rostrhamus sociabilis plumbeus*), cactus bugs [*Chelinidea vittiger* (Fletcher et al. 2011)], the damselfly *Indolestes peregrinus* (Kadoya and Washitani 2012), the logrunner [*Orthonyx temminckii* (Pavlacky et al. 2012)] and the endangered Iberan lynx [*Lynx pardinus* (Ferreras 2001)]. Moreover, an individual-based model developed by Gustafson and Gardner (1996) showed that altering landscape heterogeneity resulted in asymmetric rates of immigration and emigration among resource patches. Hence, asymmetric connectivity may be the rule more than the exception, given that symmetric connectivity may only be applicable for organisms where dispersal is not affected by advection sources, spatial variation in resources, or that live in homogeneous landscapes. Such examples are likely to be uncommon in nature.

The lack of recognition of asymmetric connectivity in empirical metapopulation studies may be due in part to the absence of an estimation framework that can incorporate asymmetric dispersal. Here we provide a simple framework using dynamic occupancy modeling coupled with asymmetric connectivity as a covariate. The asymmetric connectivity measure that we applied can be generally used with other simple advection sources (e.g., water current direction). Wind direction can also be replaced by the angle of riverine or marine currents. We expect that the incorporation of asymmetric connectivity into metapopulation modeling will provide more reliable conclusions regarding the role of connectivity, potentially increase the accuracy of conservation and management decisions (Beger et al. 2010), and may reveal connectivity effects where they were previously assumed to be negligible (e.g., Winfree et al. 2005; Pellet et al. 2007).

Author contribution statement M. A. A. and R. J. F. designed the study; R. L. T. and E. M. A. performed the study; M. A. A. analyzed the data; M. A. A., R. J. F., R. L. T., and E. M. A. wrote the manuscript.

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