The role of seasonality and non-lethal carry-over effects on density-dependent dispersal

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Abstract. Understanding dispersal is critical for predicting a wide range of ecological dynamics. Variation in intraspecific density is widely regarded as a major factor influencing dispersal rates but it is not clear why dispersal is positively related to density in some systems and negatively related to density in other systems. Using seasonal populations of *Drosophila melanogaster*, we experimentally show that dispersal rates are both positively related to breeding density at the time of dispersal and negatively related to density at the beginning of the previous non-breeding season. This suggests that flies use density at the time of dispersal as a cue for habitat quality but are also negatively influenced by the delayed, non-lethal effects of density in the previous season. A parameterized model indicates that a carry-over effect not only causes a decrease in the proportion of individuals that disperse, but also a decrease in population size caused by lower per capita breeding output. Our results demonstrate how density can have contrasting effects on dispersal and population size depending on when density is measured in the annual cycle and that non-lethal effects on individuals can have important, but previously unrecognized, consequences for both the movement rates and long-term dynamics of seasonal populations.

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INTRODUCTION

The movement of individuals in space and time is widely recognized as critical for predicting the dynamics of populations (Levins 1969, Hanski 1999), the structure of communities (Levine and Murrell 2003, Cottenie 2005, Holyoak et al. 2005), and the spread of species invasion (Neubert and Caswell 2000, Ellner and Schreiber 2012, Perkins et al. 2013). A common expectation regarding movement is that dispersal rates increase as environmental conditions within a population deteriorate (Travis et al. 1999, Innocent et al. 2010), which leads to the prediction that dispersal should increase with intraspecific density (positive density-dependent dispersal; Travis et al. 1999, Innocent et al. 2010). Although this prediction has been supported by several studies (Matthysen 2005, Clobert et al. 2009, Meester and Bonte 2010), it has also been shown that dispersal can decrease with density (negative density-dependent dispersal; Herzig 1995, Matthysen 2005, Støen et al. 2006, Meylan et al. 2007). Interestingly, empirical observations suggest that, in seasonal environments, where density can operate in more than one season (Fretwell 1972, Ratikainen et al. 2008), dispersal is often negatively related to density (Ims and Andreassen 2005, Matthysen 2005), suggesting that temporal variation in resources (e.g., seasonality) is a key factor to understand density-dependent dispersal (Wahlström and Liberg

1995, Morris and Diffendorfer 2004, Matthysen 2005, Rodrigues and Johnstone 2014). Although some hypotheses have been proposed to explain this phenomenon (e.g., the 'social fence' hypothesis; Hestbeck 1982), there is little empirical support for a mechanism driving a negative relationship between density and dispersal.

One mechanism that could drive a negative relationship between density and dispersal is a density-mediated carry-over effect. Density-mediated carry-over effects occur when density in one season influences the performance of individuals that survive to the following season (Harrison et al. 2011, Betini et al. 2013a). Recent evidence from seasonal populations of *Drosophila melanogaster*, the common fruitfly, has shown that variation in density at the beginning of the non-breeding season negatively influences reproductive output of females that survive to the following breeding season (Betini et al. 2013b). The mechanism driving this density-mediated carry-over effect is through variation in physiological condition: individuals spending the non-breeding season at high density weigh less entering the breeding period compared to individuals that spend the non-breeding season at low density (Betini et al. 2013b). At the population level, including density-mediated carry-over effects in a statistical model significantly improves the ability to predict variation in per capita breeding rates over 23 generations (Betini et al. 2013b) and there is evidence that this carry-over effect can stabilize long-term dynamics (Betini et al. 2013a). Although these results point to the importance of non-lethal effects on the dynamics of seasonal populations, there is no evidence of how density-mediated carry-over effects might influence dispersal because all experiments were conducted on closed populations (i.e., no immigration or emigration). If density mediated carry-over effects influence individual dispersal rates, it could provide an important causal link between the negative relationship between density and dispersal because virtually all populations live in seasonal environments.

Here, we use simulated seasonality in *D. melanogaster* to experimentally examine the hypothesis that density-mediated carry-over effects influence the probability of dispersal through its effect on individual condition. We predicted that,

while controlling for breeding density just prior to the dispersal event, dispersal rate would be negatively related to density at the beginning of the previous non-breeding season. We then developed a with season specific parameters to show how such density-mediated carry-over effects on dispersal can potentially affect the dynamics of populations.

MATERIALS AND METHODS

Study system

As in Betini et al. (2013a, b), we simulated seasonality in *D. melanogaster* by changing food composition. The 'non-breeding season' (duration: 4 d) consisted of an empty plastic vial (28 × 95 mm) and a pipette tip that was filled with 0.2 mL of 5% water–sugar solution each day, which provided food but prevented egg-laying. For the 'breeding season' (duration: 17 d), adults were placed in same-size vials but with 10 mL of dead sugar-yeast medium that was used as food and an egg-laying substrate. Adults were allowed to lay eggs for 24 hrs (day 0), after which they were discarded and larvae were allowed to mature to adults. For additional details on this 'seasonal' system, see Betini et al. (2013a).

Dispersal experiment

To examine the effects of density at the beginning of the non-breeding season (hereafter termed '*non-breeding density*') and at the beginning of the breeding season (hereafter termed '*breeding density*') on dispersal, we conducted an experiment using three non-breeding density treatments and three breeding density treatments (Fig. 1). To control for variation in body size and age, we used offspring from parents that bred at low density to source the non-breeding groups (Sang 1949): 10 males and 10 females were allowed to lay eggs for 24 h in a vial with 10 mL of dead sugar-yeast medium. Flies were introduced into the non-breeding season vials at densities of 20 ($n = 320$ replicates or vials), 180 ($n = 42$), or 300 ($n = 77$). After the non-breeding season, survivors from each of these density treatments were lightly anesthetized with CO_2 and moved to breeding season vials at densities of 10, 80, or 180 (50:50 sex ratio). Individuals from the same non-breeding density treatment were pooled before being moved to the breeding
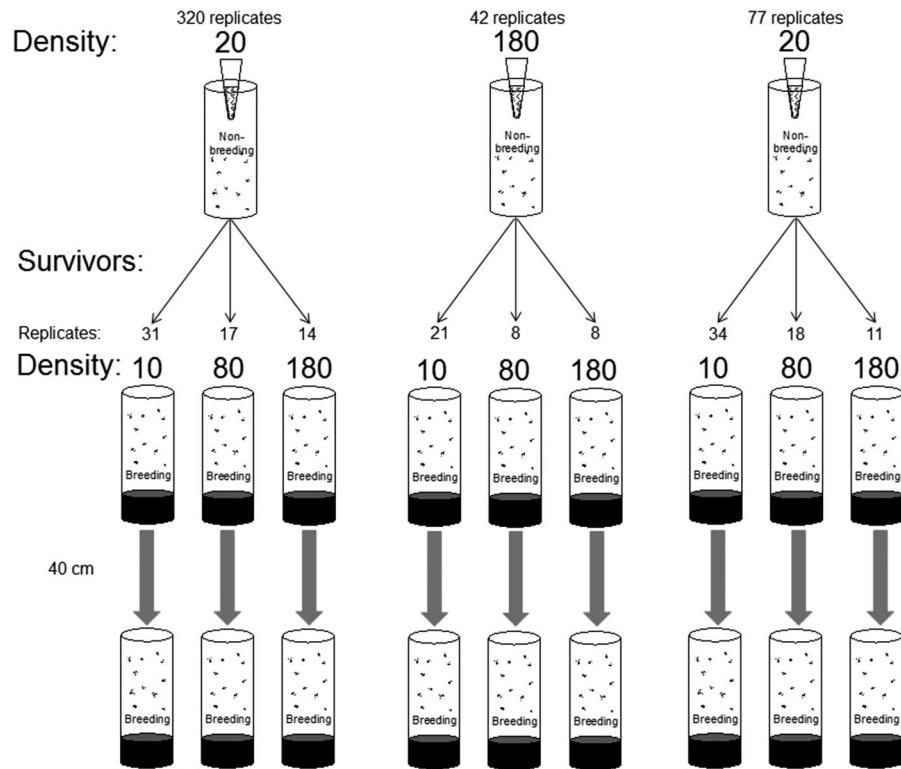
Fig. 1. Schematic diagram of dispersal experiment. Breeding vials were connected to a peripheral breeding vial via 40 cm long tube. Once they were introduced to the primary breeding vial, flies were free to move to the peripheral vial but could not move back to the original vial.

season to reach the requisite number of flies for a given breeding density treatment and to control for potential differences between non-breeding vials (Fig. 1). For breeding density = 10, we used 31, 21 and 34 replicates for each of the three non-breeding density treatments (i.e., 20, 180 and 300, respectively). For breeding density = 80, sample sizes for the three non-breeding density treatments were 17, 8 and 18, and for breeding density = 180, sample sizes were 14, 8 and 11 (Fig. 1).

Prior to the introduction of flies to the breeding season vials, we connected a second breeding season vial (termed "*peripheral vial*") to each original vial using a 40 cm tube (0.8 cm diameter; Fig. 1). We placed a pipette tip (~0.2 cm diameter) at the end of this tube, so that flies could not return to the original vials once they moved to the peripheral vial. Thus, once flies entered the breeding season, they could either stay in the original breeding vial or move through the tube to the peripheral vial. After 24 h, the

number of individuals that moved to the peripheral vial was counted to measure the proportion that dispersed. All stages of the experiment were performed at 25°C, 12 h light:12 h dark light cycles, with humidity between 30% and 50%.

To determine whether breeding density (density at the time of dispersal) and non-breeding density (i.e., carry-over effect) influenced the proportion of flies that dispersed, we used a generalized linear model with a binomial distribution and logit link function. The proportion of flies that dispersed was entered as a response variable and density at the beginning of the non-breeding and breeding season as explanatory variables. We tested the significance of each explanatory variables by comparing a model with and without each variable using a *F*-test (Crawley 2013). Parameters were estimated using maximum likelihood.

The model

To examine the potential consequences of a

density-mediated carry-over effect on dispersal, we developed a logistic population model with season specific parameters. Consistent with the experimental design outlined above, we assumed that dispersal occurred just after the beginning of the breeding season, but prior to when flies start to breed. Therefore, population size at the end of each season was determined by an intrinsic growth rate or survival (breeding or non-breeding season) and the within-season density dependent effect such that

$$Y_{t+1} = X_t \times sa \times exp(b \times X_t) \tag{1}$$

$$X_{t+1} = (Y_{t+1} - D_{t+1}) \times ra \times exp[a \times (Y_{t+1} - D_{t+1})] \tag{2}$$

where Y_t and X_t are, at generation t, population size at the end of the non-breeding and breeding season, respectively. Terms sa and ra are the intrinsic finite rates of survival and growth, and b and a, are the density dependence effects on survival and breeding, respectively. D_{t+1} is the number of individuals that disperse just prior to breeding and, in the absence of carry-over effect, is a function of the density at the beginning of the breeding season, such that

$$D_{t+1} = f(Y_{t+1}). \tag{3}$$

To incorporate carry-over effects on dispersal in the model, we made D_{t+1} also a function of the number of individuals that start the non-breeding season in the previous season, such that

$$D_{t+1} = f(Y_{t+1}, X_t). \tag{4}$$

We estimated ra, sa, a and b for both seasons using data from Betini et al. (2013a), where we simulated seasonality in *D. melanogaster* the same way described here. Briefly, we placed individuals at the breeding and non-breeding season at different densities to estimate the intrinsic growth rate and survival rate and the strength of density dependence in each season (Betini et al. 2013a). To obtain these parameter values, we fit an exponential curve to the data using the *nls* function in R (R Core Team 2015; Table 1), where

$$per\ capita\ breeding = ra \times exp(a \times Y_t) \tag{5}$$

$$per\ capita\ survival = sa \times exp(b \times X_t) \tag{6}$$

where per capita breeding and per capita survival were calculated as the number of individuals at the end of each season divided by the number of individuals that started the season.

Eqs. 3 and 4 were obtained using a multiple linear regression where the response variable was the number of individuals that moved and the predictor variables were density at the beginning of the breeding and non-breeding season, and their interaction (see Results). We used Eqs. 1, 2 and 3 to investigate the dynamic of populations when dispersal was solely a function of density at the beginning of the breeding season (the '*dispersal model*'). We calculated the population size at the end of the breeding and non-breeding seasons, the proportion of individuals that dispersed (number of individuals that dispersed divided by the number of individuals that started the breeding season) and per capita breeding output (number of individuals at the end of the breeding season divided by the number of individuals at the beginning of the breeding season after dispersal). Population size was calculated at the end of the breeding season when population reached equilibrium (i.e., $Y_{t+1} = Y_t$ and $X_{t+1} = X_t$). We then replaced Eqs. 3 for 4 to obtain the same metrics when dispersal is also influenced by density-mediated carry-over effects (the '*carry-over effect model*'). Finally, we investigate how the strength of carry-over effect on dispersal could influence population dynamics by manipulating the strength of carry-over effect on dispersal. To do this, we changed the parameter that governed the effect of the interaction between the breeding and non-breeding densities on the number of individuals that dispersed.

RESULTS

The number of individuals that dispersed was a good fit compared to observed values (whole model test: log likelihood: 12.7, $\chi^2 = 25.4$, $n = 161$, df = 2, $p < 0.001$); predicted values explained 64% of the variation in observed values ($R^2 = 0.64$, $\beta = 0.65$, SE = 0.04, $t = 16.6$, $p < 0.0001$). Both breeding density at the time of dispersal ($F_{158, 159} = 159.6$, $p < 0.001$) and density in the previous non-breeding season ($F_{158, 159} = 49.1$, $p < 0.001$) were significant predictors of the proportion of flies dispersing to the peripheral vial. There tended to be a positive relationship between

Table 1. Parameters estimated with our experimental results and used in our *dispersal* and *carry-over effect* models to predict dispersal, population size and per capita breeding output.

Season	Parameter	Estimate	SE	t	P
Breeding	ra	12.53	9.93×10^{-1}	12.61	<0.001
	a	-1.27×10^{-2}	2.84×10^{-3}	-4.47	<0.001
	d	6.18×10^{-2}	1.43×10^{-2}	42.93	<0.001
Non-breeding	sa	9.45×10^{-1}	9.70×10^{-3}	97.11	<0.001
	b	-6.30×10^{-4}	8.66×10^{-5}	-7.27	<0.001
	e	-2.62×10^{-2}	5.43×10^{-3}	-4.82	<0.001
Interaction	g	-4.94×10^{-4}	8.44×10^{-5}	-5.85	<0.001

dispersal rates and breeding density but a negative relationship between dispersal rate and density at the beginning of the previous non-breeding season (Fig. 2).

The number of individuals that dispersed as a function of the breeding and non-breeding densities was estimated as

$$c + d \times Y_{t+1} + e \times X_t + g \times Y_{t+1} \times X_t \qquad (7)$$

where c is the intercept of the relationship between the number of individuals that moved and the breeding density treatments and d, e and g are the slopes of the effect of the density at the

beginning of the breeding (d) and non-breeding (e) densities, and their interaction (g; Table 1). We set c to 0 because we assumed that at very low breeding densities there would be no dispersal.

To calculate population size at the end of each season when dispersal was influenced by both the density at the beginning of the breeding season (the '*carry-over effect model*'), we replaced D_{t+1} in Eq. 2 by Eq. 7. The effects of breeding density on dispersal was also calculated with Eq. 7, but X_t was set to zero (the '*dispersal model*').

As expected, density-mediated carry-over effect had a negative impact on the proportion of individuals that dispersed when populations where at equilibrium (Fig. 3A). This effect was stronger as the carry-over effect on dispersal increased (i.e., for more negative values of g; Fig. 3A). The density-mediated carry-over effect on dispersal decreased population size (Fig. 3B) and per capita breeding output (Fig. 3C) and these effects were also stronger as the strength of the carry-over effect on dispersal increased (i.e., for smaller values of g; Fig. 3C). A strong carry-over effect destabilize dynamics by moving the population equilibrium from a stable dynamic to a two-point cycle where population fluctuated regularly between two values within each season (Fig. 3C).
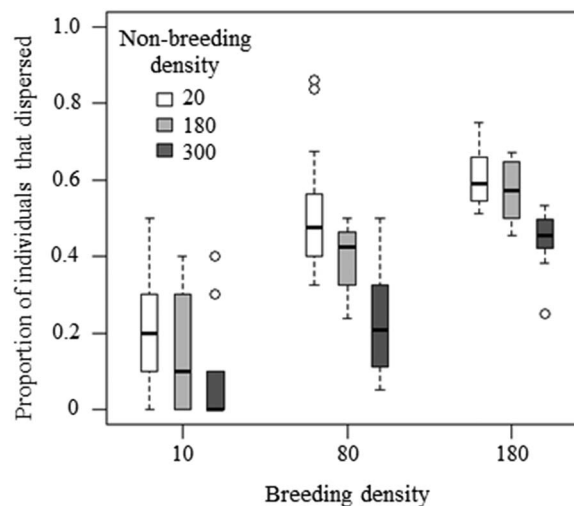
DISCUSSION

Fig. 2. Results from the experiment showing the proportion of *Drosophila melanogaster* dispersing to a peripheral vial just after the start of the breeding season in relation to breeding density (*x*-axis) and density at the beginning of the previous non-breeding season (shaded bars), the latter of which is a density-mediated carry-over effect. Both breeding and non-breeding season density were significant predictors of dispersal (see *Results*).

The results of our experiment provide clear evidence of how density can have contrasting effects on dispersal depending on when density is measured relative to dispersal over an individual's life-cycle. Although density at the time of dispersal ('breeding density') had a strong positive effect on dispersal rate, there was also a negative relationship between density at the beginning of the previous non-breeding season
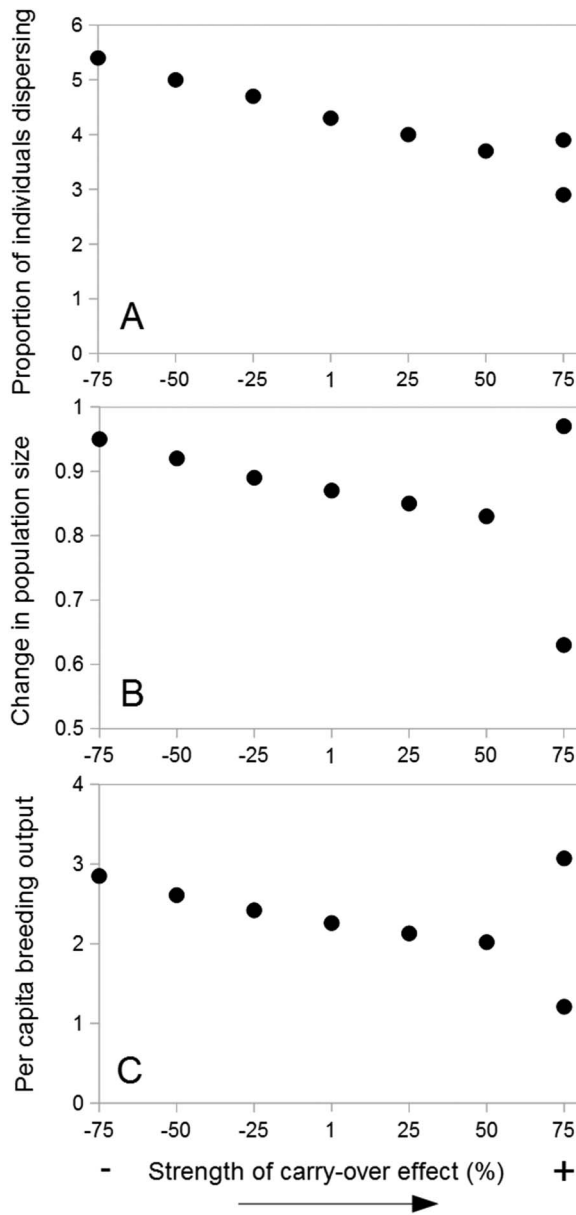
Fig. 3. Population consequences of density-mediated carry-over effect on dispersal. The strength of carry-over effect (non-breeding density) on dispersal (*x*-axis) was manipulated by increasing (positive values in the *x*-axis) or decreasing (negative values) the parameter *g* by 25, 50 or 75% (1 represents the value of *g* as estimated with our experimental data; see Table 1). Panels show the strength of the carry-over effect in relation to (A) the proportion of individuals dispersing from the population (B) change in population size (calculated with respect to the value from a model when dispersal was only influenced by the breeding

and dispersal (i.e., carry-over effect). In the former case, density appeared to act as a cue about the state of the habitat at the time of dispersal (i.e., a high proportion of individuals leaving the original habitat at high density because of a perceived decline in suitability). In the latter case, high non-breeding density likely decreased physiological condition of the individuals that survived to enter the breeding season (Betini et al. 2013*a*, *b*) and individuals in poor condition would be less willing to move (Ims and Hjermann 2001). These opposing effects on dispersal emphasize the significance of documenting variation in density across multiple stages of the annual cycle (Morris and Diffendorfer 2004, Betini et al. 2013*b*). In systems where both delayed and direct effects of density act on dispersal (e.g., in seasonal environments), the causes of dispersal may be misinterpreted or even missed if there are only data on density available at or near the time of dispersal.

Although not directly measured in this experiment, the mechanism linking dispersal rate with non-breeding density in the previous season is most likely variation in individual condition. In recent studies, we have shown the variation in density during the non-breeding season influences the dry weight of flies surviving to enter the breeding period (Betini et al. 2013*b*), which then carries over to influence reproductive output (Betini et al. 2013*a*). However, in other populations, the decision to disperse could also be influenced by past densities acting through other mechanisms (Morris and Diffendorfer 2004), such as maternal effects (Bitume et al. 2014), access to mates (Stamps 1991), aggressive interactions (Hestbeck 1982), mating status (Simon et al. 2011), foraging behavior (Edelsparre et al. 2014), or competitive environment (Innocent et al. 2010). For example, individuals may be more willing to disperse in a given season if their assessment of the competitive environment is

(continuation of Fig. 3 caption)
density [the *dispersal model*]) and (C) per capita breeding output. Population size was calculated at the end of the breeding season when population reached equilibrium. The two values at 75% indicate that the population moved from a stable dynamic to a 2-point cycle (see *Results* for details).

based on density in the previous season. Although our experiment suggests that physiological condition, as influenced by density, could carry-over to the following season to negatively affect movement, the precise delayed mechanisms affecting dispersal and whether this will relate positively or negatively to dispersal is likely to be context- and species-dependent.

According to our population model, density mediated carry-over effects on dispersal could impact populations in a way that has not been previously explored. In single population models, the removal of individuals by dispersal usually causes populations to increase (Ruxton 1995). Our results suggest that a density-mediated carry-over effect could reduce the number of individuals dispersing, causing a decrease, not a increase, in population size. This happened because, compared to our dispersal model, the carry-over effect negatively impact the number of individuals leaving the population. As a consequence, more individuals bred, which resulted in a strong negative feedback on per capita breeding output caused by density dependence and, potentially, a destabilizing effect on the dynamics of single populations. This suggests that the results of our population model might be robust only for species with high fecundity or those that are strongly regulated by density dependence. Thus, the population consequences of density-mediated carry-over effect on dispersal is likely to vary with the kind of life history strategy of the organism, which has the potential to affect vital rates and population dynamics (Sæther et al. 2002, Herrando-Pérez et al. 2012).

A reduction in dispersal rates through a density-mediated carry-over effect could have important impact on population dynamics beyond those shown by our model. For example, a reduction in dispersal rates could synchronize demes within a metapopulation and, therefore, lead to more stable dynamics. Although this prediction is consistent with some studies (Dey and Joshi 2006), the role of dispersal in structuring population and community dynamics is complex (Ims and Andreassen 2005, Cadotte 2006, Clobert et al. 2009). For example, there is evidence that dispersal might not influence population synchrony (Ims and Andreassen 2005, Griffen and Drake 2009), or that the impact of synchrony on population dynamics might be context-dependent (Steiner et al. 2013). Moreover, low dispersal rates can hamper 'rescue effects' (Brown and Kodric-Brown 1977) and result in low species diversity (Cadotte 2006). Regardless of the ultimate effect of dispersal on ecological systems, our results provide strong evidence for a mechanism by which density can have a negative effect on dispersal, demonstrates that carry-over effects can impact individual movement, and indicates how these non-lethal effects can influence population dynamics.

Given that dispersal can be energetically costly (Bonte et al. 2011), delayed effects of density on dispersal caused by temporal variation in resources could be a widespread, but underappreciated, phenomenon (Morris and Diffendorfer 2004, Debeffe et al. 2012, Bitume et al. 2014). This is particularly important because humans are creating an increasingly disturbed and fragmented landscape, and it is widely recognized that the persistence of a species relies on the ability to explore and move through the landscape (Parmesan 2006, Swift and Hannon 2010, Post 2013).

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