LETTER

Experimental evidence for the effect of habitat loss on the dynamics of migratory networks

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Abstract

Migratory animals present a unique challenge for understanding the consequences of habitat loss on population dynamics because individuals are typically distributed over a series of interconnected breeding and non-breeding sites (termed *migratory network*). Using replicated breeding and non-breeding populations of *Drosophila melanogaster* and a mathematical model, we investigated three hypotheses to explain how habitat loss influenced the dynamics of populations in networks with different degrees of connectivity between breeding and non-breeding seasons. We found that habitat loss increased the degree of connectivity in the network and influenced population size at sites that were not directly connected to the site where habitat loss occurred. However, connected networks only buffered global population declines at high levels of habitat loss. Our results demonstrate why knowledge of the patterns of connectivity across a species range is critical for predicting the effects of environmental change and provide empirical evidence for why connected migratory networks are commonly found in nature.

Keywords

Climate change, *Drosophila melanogaster*, graph theory, migratory connectivity.

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INTRODUCTION

Organisms are often distributed in time and space over a series of subpopulations interlinked by the movement of individuals (Levins 1969; Hanski 1998). Migratory species are a special case of this spatial and temporal variation because they are typically distributed over a series of interconnected breeding and non-breeding sites that are occupied at distinct periods over the course of an annual cycle (Fancy *et al.* 1989; Webster *et al.* 2002; Taylor & Norris 2010; Allen *et al.* 2013; Kennedy *et al.* 2013; Flockhart *et al.* 2015). In most cases, individuals originating from one site in a given season migrate to multiple sites in the following season (Kennedy *et al.* 2013; Wiederholt *et al.* 2013), causing breeding and non-breeding sites to become demographically linked through the exchange of individuals across seasons (Taylor & Norris 2010). Understanding how this spatial and temporal demographic structure influences population dynamics is critical for determining how migratory populations will response to environmental change (Martin *et al.* 2007; Bowlin *et al.* 2010) and is particularly relevant given that many migratory populations have experienced severe declines in recent decades (Wilcove & Wikelski 2008).

Borrowing terminology from mathematical graph theory, Taylor & Norris (2010) proposed that migratory populations could be represented as a *migratory network* (Fig. 1; see also Sutherland & Dolman 1994; Dolman & Sutherland 1995; Marra *et al.* 2006), consisting of a series of bipartite *nodes* (subpopulations with distinct classes, e.g. breeding or non-breeding sites) in which individuals must use at least one node in each class over the course of the annual cycle (Fig. 1). Individuals move between classes of nodes by migrating along undirected *edges*, which are migratory routes that can be travelled in both directions (Fig. 1). The migratory network approach is potentially very powerful because it can be applied to virtually any migratory system (e.g. Sutherland & Dolman 1994; Flockhart *et al.* 2015; Wiederholt *et al.* 2013; James & Abbott 2014) and it generates explicit hypotheses and testable predictions about how the whole network, as well as the nodes and edges within the network, should respond to environmental change.

One hypothesis is that, assuming all nodes within a season are initially of equal carrying capacity, habitat loss at a single node will cause more edges to be populated within the network due to density-dependent compensation effects (the '*mixing hypothesis*'; Fig. 1a–c). For example habitat loss at a single non-breeding node (e.g. NB1, Fig. 1) will result in fewer individuals leaving that node at the end of the season. Assuming that migratory mortality is proportional to distance, the breeding node that will experience the strongest decline in population size is B1 (Fig. 1), i.e. the closest breeding node to the node where habitat loss happened. With fewer individuals arriving at B1 from NB1 and no changes in carrying capacity, there will be more resources available at B1 for individuals originating from other non-breeding nodes (NB2 and NB3, Fig. 1). Thus, population size at edges linking B1 to NB2 and NB3 should increase. Put another way, heterogeneity among nodes within a season is predicted to result in a higher degree of connectivity within the network (Taylor & Norris 2010).

A second hypothesis is that a perturbation at a single node within a connected network will have demographic effects on other nodes throughout the network even if they are not directly connected to that node by migrating individuals (the '*knock-on effect hypothesis*'). For example habitat loss at a single non-breeding node will decrease population size at the
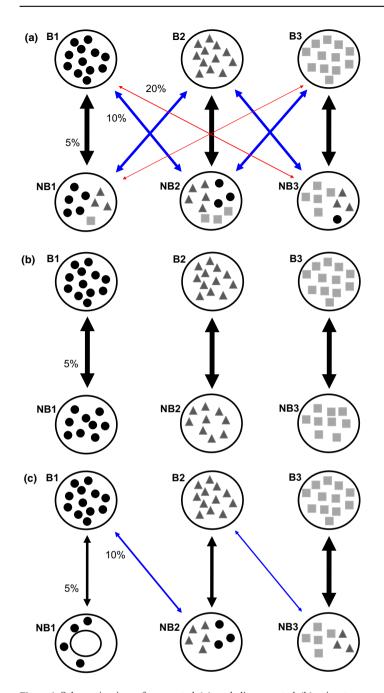
Figure 1 Schematic view of connected (a) and disconnected (b) migratory networks with three breeding nodes (B1, B2 and B3) and three non-breeding nodes (NB1, NB2, NB3). Heterogeneity created by habitat loss in one of the wintering nodes (c) could generate routes that would not exist in a homogeneous network. The width of the arrows indicates the number of individuals moving between breeding and non-breeding nodes and the length of the arrow indicates the distance between nodes. In the shortest distance (black arrows), migratory mortality is 5, 10% for the medium distance (blue arrows) and 20% for the longest distance (red arrows).

breeding nodes, releasing individuals from negative density dependence effects and causing the number of individuals in the other non-breeding nodes to increase (Fig. 1a, c). Although a perturbation at a single node may influence all nodes within a network, the magnitude of this change in terms of population size should be negatively related to the

distance between a given node and the node in which the perturbation took place (Taylor & Norris 2010).

Finally, an important hypothesis from these models is that connected networks, where individuals mix between breeding and non-breeding nodes, will buffer global (whole network) population declines arising from environmental change compared to disconnected networks, where individuals do not mix between breeding and non-breeding nodes. This is predicted to occur because connected networks have a greater capacity to absorb losses through density-dependent feedback mechanisms at multiple nodes (Dolman & Sutherland 1995; Marra *et al.* 2006; Taylor & Norris 2010). For example in a disconnected network, habitat loss at one non-breeding node will only cause declines at this node and in the connected breeding node (Fig. 1b). In this case, global population decline is equal to the population decline at these two migratory nodes. However, in a connected network, habitat loss at a single site can increase the degree of connectivity within the entire network, which increases the number of individuals at the non-breeding sites where there were no changes in habitat, and results in less of an overall decline in the network. Although these hypotheses about how migratory networks should respond to habitat loss generate a number of explicit predictions, they have never been directly tested.

To experimentally examine these hypotheses, we used non-overlapping populations of the common fruit fly (*Drosophila melanogaster*) submitted to temporal variation in resources (i.e. seasonality; Betini *et al.* 2013a,b) and added spatial variation to create replicated connected and disconnected networks consisting of three breeding and three non-breeding nodes of equal quality within a season (Fig. 1a, b). We applied mortality during migration that was proportional to the length of an edge (distance between nodes; Fig. 1c) and, after 11 generations, simulated habitat loss at a single non-breeding node in half of the replicates in both the connected and disconnected networks. We counted individuals at the end of each season and evaluated the changes in population size over time in the control replicates and in the 'habitat loss' replicates.

METHODS

Study system

Our previous work used temporal variation in resources to simulate breeding and non-breeding periods in laboratory populations of *D. melanogaster* to understand the dynamics of single populations in a seasonal environment (Betini *et al.* 2013a,b). In this study, we use this 'seasonal' treatment and then add spatial variation in population structure to simulate a migratory network. Both the temporal and spatial treatments are described below.

Temporal variation in resources: breeding and non-breeding periods

To simulate seasonality in lab populations of *D. melanogaster*, we changed food composition to generate two distinct 'seasons' (Betini *et al.* 2013a,b). During the 'breeding season', flies were allowed to lay eggs for 24 h (day 0) in a dead yeast–sugar medium, after which the adults were discarded and eggs

were allowed to hatch and mature to adulthood. Offspring were moved from old to fresh food vials every 2 days from day 10 to 16 to avoid high offspring mortality (Dey & Joshi 2006). During this period, densities of offspring were not manipulated, i.e. their densities were a function of the number of flies that emerged in each vial. On day 17, offspring were lightly anaesthetised with CO_2, counted and placed into the non-breeding vials for 4 days. The 'non-breeding season' consisted of an empty vial of the same size as the breeding vials and a pipette tip filled with 0.200 mL of 5% water–sugar solution per day. This medium provided food for the flies but prevented egg-laying (Bownes & Blair 1986). Because the food is kept constant in both seasons, the system is governed by direct and delayed density dependence, the latter caused by non-lethal carry-over effects (Betini *et al.* 2013a,b). The number of days in each season was determined based on the optimal duration in which vital rates were influenced by density dependence (Betini *et al.* 2013a), which is an important feature of many migratory systems (Runge & Marra 2005; Fryxell & Holt 2013; Lok *et al.* 2013).

Spatially structured populations: the migratory network

A fully connected migratory network is one in which a portion of individuals from each node (or site) in one season migrate to all other nodes in the subsequent season (Taylor & Norris 2010). For our experiments, we simulated both connected and disconnected networks using three breeding and three non-breeding nodes and then simulated habitat loss at a single node in both types of networks (Fig. 1a, c). This allowed us to examine the effect of habitat loss on what is viewed as a 'typical' situation for a migratory organism in which there is mixing between breeding and non-breeding nodes (i.e. connected network) vs. a control (i.e. disconnected network; Fig. 1b).

We simulated a connected network by moving individual flies from the same breeding node to three different non-breeding nodes and then moving the survivors back to their original breeding nodes (Fig. 1a). We chose this approach rather than letting individuals randomly move between breeding and non-breeding nodes because most migratory animals show high site fidelity to both their breeding and non-breeding sites (Leggett 1977; Serneels & Lambin 2001; Shizuka *et al.* 2014). Furthermore, individuals typically follow the same migratory route over their lifetime (Leggett 1977; Serneels & Lambin 2001; Delmore & Irwin 2014) and there is evidence that migratory pathways are heritable (Pulido 2007; Liedvogel *et al.* 2011; Delmore & Irwin 2014; Shizuka *et al.* 2014), which implies that, in many species, migratory routes are conserved over multiple generations.

We began our experiments in the breeding season with 60 randomly selected vials that were kept in the same size vials and using the same protocol as described above for the breeding season. Individuals were only moved to different nodes between seasons, never within season. In the connected network, this means that individuals from each node could take one of three edges (migratory routes) available. For example individuals in the breeding node 1 (B1) could be assigned to

edges B1 → NB1, B1 → NB2 or B1 → NB3 (Fig. 1a). Likewise, by the end of the non-breeding season, survivors were moved back to the breeding season using edges NB1 → B1, NB2 → B1 or NB3 → B1 (Fig. 1a). Because individuals from different breeding nodes were mixed in a single non-breeding vial, we marked all individuals from each breeding node so that we could identify their origin by the end of the non-breeding season. To do this, on day 16 (last day of the breeding season), we marked all offspring from each breeding vial with a small amount of dry fluorescent pigment (DayGlo) of different colour (red, blue or yellow). After grooming overnight in larger bottles (177.4 mL) with 20 mL of food most of the pigment had been removed except for a small 'badge' on their ventral and dorsal thorax. On the morning of day 17, flies were lightly anaesthetised with CO_2, counted and placed into the non-breeding vials. To control for potential effects of pigment colour on survival and reproduction, we randomly selected a pigment colour for each breeding node each generation.

In the first generation, the number of individuals at the end of the breeding season in each edge was determined by dividing the number of individuals in each breeding node by 3, and then removing 5, 10 or 20% according to the migratory distance of each edge (i.e. we assumed that migratory mortality is a function of distance between nodes; Alerstam & Lindström 1990; Alerstam *et al.* 2003; Ardia 2005), and placing them into the non-breeding vials. These mortality parameters were based on empirical estimates from natural systems (Sillett & Holmes 2002; Strandberg *et al.* 2009; Klaassen *et al.* 2013). After 4 days in the non-breeding season, we lightly anaesthetised the survivors from each vial with CO_2, identified their colour (i.e. breeding origin), applied the migratory mortality according to the migratory distance and placed them back into the breeding vials with fresh food. As in the standard seasonal protocol described above, these survivors had 24 h to lay eggs, and these progeny were allowed to develop to adulthood.

For the second generation onward, the number of flies moved to each non-breeding vial was proportional to the number of survivors in the previous generation; i.e. we assumed an ideal free distribution were individuals have the same reproductive potential. The number of flies in each edge at the end of the breeding season was calculated by multiplying the per capita growth rate of a node by the number of individuals that occupied a single edge and then multiplying by the appropriate migratory mortality parameter:

$$X_{ij}(t) = \left(\frac{Xo_{i(t)}}{Xo_{(t-1)}} * Y_{ij(t-1)}\right) * m_{ij} \tag{1}$$

where $X_{ij(t)}$ is the number of individuals in edge ij at the end of the breeding season at generation t after migration, $Xo_{i(t)}$ is the number of individuals in node i at the end of the breeding season in generation t, $Xo_{i(t-1)}$ is the number of individuals in node i at the beginning of the breeding season in generation $t - 1$, $Y_{ij(t)}$ is the number of individuals in edge ij at the end of the non-breeding season at generation t after migration and m_{ij} is migratory mortality for each edge ij (Fig. 1a). This procedure was repeated for 24 generations in 20 replicates of

connected networks, each with three breeding and three non-breeding nodes (Fig. 1b).

To simulate a disconnected network with three breeding and three non-breeding nodes, we used the same protocol described above, except that only one edge connected each node and there was no mixing of individuals between nodes, i.e. individuals in breeding node B1 only went to non-breeding node NB1 (Fig. 1b). Migratory mortality was 5% for all edges, which is the same migratory mortality for the edges connecting the closest nodes in the connected network. We used this mortality because we wanted to compare global population size of connected and disconnected networks. This procedure was repeated for 24 generations in 18 replicates of disconnected networks, each replicate with three breeding and three non-breeding nodes. We also marked individuals with the same fluorescent pigments we used in the connected network, so that potential differences in vital rates caused by the pigment used would affect both types of networks similarly.

We simulated habitat loss in both the connected and disconnected networks by removing 30% of the daily amount of food in the non-breeding node NB1 in generation 11 in half of our replicates ($n = 10$ for connected network and $n = 9$ for unconnected network; Fig. 1c).

To investigate the long-term consequences of habitat loss on migratory networks, we also developed a deterministic bi-seasonal model (i.e. using season-specific parameters). We parameterised the model with results from our experiments and ran simulations until they reached equilibrium. Details of the model can be found in the Supporting information.

Statistical analysis

To test whether habitat loss at a single non-breeding edge could increase the degree of connectivity (the *mixing hypothesis*), we used generalised mixed effect models (GLMMs) with number of individuals at the end of each season in each edge as a response variable and the interaction between treatment (i.e. habitat loss or control) and generation as explanatory variables. We considered that habitat loss caused an impact in the population size if the change in population size was different between habitat loss and control replicates (significant interaction between '*treatment*' and '*generation*') and/or population size after habitat loss was, on average, different between habitat loss and control replicates (explanatory variable '*treatment*' was significant). Because we have several replicates for each type of network (i.e. a set of three breeding and three non-breeding nodes that formed the network) and each node was sampled repeatedly over 24 generations, we entered node and generation as random effects (i.e. uncorrelated random intercept and random slope within node) to control for potential differences among nodes in different network replicates.

To test for changes in population size in each node (the *knock-on effect hypothesis*), we used a similar approach described above for the *mixing hypothesis*, but using linear mixed effect models (LMMs) and population size at the end of each season, in each node as a response variable. To test the *buffer hypothesis*, we used a LMM with the same random structure as described above, but global population size as a response variable and generation and the interaction between

kind of network and treatment (i.e. habitat loss or control) as explanatory variables. Global population size was calculated by first adding population size at the end of each season in each node for each network (three breeding and three non-breeding nodes in each replicate) and then averaging this number by the number of network replicates ($n = 10$ for each habitat loss and control replicates in the connected network and $n = 9$ for each habitat loss and control replicates in the disconnected network).

Preliminary analysis showed that the number of individuals at the end of both the breeding and non-breeding season in each edge or node was not significantly different between control and treatment before we imposed habitat loss (Tables S2–S5; the only exception was node B2 in the disconnected network where population size was 13% higher in the habitat loss than in the control; $P = 0.027$, Table S5). Global population size also did not differ between control and treatment replicates (Table S6). Therefore, we only used data after the time in which we imposed habitat loss (after generation 11). We entered pigment colour as an additional explanatory variable in the models used to investigate the *mixing* and *knock-on effect* hypotheses. All LMM had Gaussian response and identity link and the GLMM had Poisson response and log link and were both fit with the *lmer* and *glmer* function from the *lme4* package in R (Bates *et al.* 2014). As a measure of goodness-of-fit, we calculated the square of the correlation between the response variable and the fitted values of each model. We standardised generation before analysis by subtracting the sample mean from each observation and dividing each value by the sample standard deviation (Schielzeth 2010). All analysis were performed in R (R Core Team 2014).

RESULTS

Overall, the results from the simulation model matched the experimental results over the 24 generations in which the experiment was run (Fig. 2 and Supporting information). As expected from the *mixing hypothesis*, habitat loss in the experiment tended to increase population size of edges B1 → NB2 (49%), B2 → NB3 (15%) and B1 → NB3, (4%) at the end of the breeding season within the connected network compared to the control (no habitat loss). Although only changes in edge B1 → NB2 were statistically significant in the experiment (Table 1; Figs 2 and 3; Table S7), the simulation model predicted that both the B1 → NB2 and B2 → NB3 edges would persist over 100 generations in the habitat loss treatment but would go extinct in the control (Fig. 2e, f). In the experiment, all other edges tended to have fewer individuals in the habitat loss treatment compared to the control. Although the decrease in population size was only significant in edges B1 → NB1, B2 → NB1 and B3 → NB2 (a reduction in population size of 21, 113 and 60% respectively; all $P < 0.05$, Figs 2b and 3c), our model results showed that, other than B1 → NB2 and B2 → NB3, all edges would go extinct by generation 40 (Fig. 2f). Analysis of the population size in each edge at the end of the non-breeding season yielded similar results (Table S8, Fig. S1).

As expected from *the knock-on effect hypothesis*, habitat loss in only one site in the connected network caused changes in
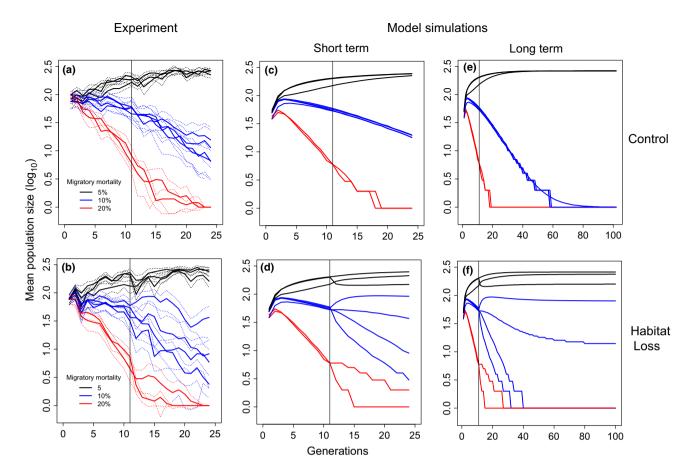
Figure 2 Mean population size ($\log_{10}$) at the end of the breeding season for 24 generations for each edge (migratory pathway) in the control (top panels) and habitat loss treatments (bottom panels) obtained from the experiment (a, b) and from a simulation model (over duration of experiment: c, d; over 100 generations: e, f). For both the simulation and experiment, all replicates for both control and habitat loss started as a fully connected network. Different colour lines represent different migratory mortalities (as in Fig. 1). The vertical grey line indicates the generation at which habitat loss was imposed in non-breeding node NB1 in treatment groups (bottom panels). For the simulation model, equilibrium was reached in generation 102 in the control (e) and generation 205 in the habitat loss treatment (f). We added 1 to the data before log transformation so that when all replicates went extinct the mean value of population ($\log_{10}$) was 0.

the population size in all nodes of the network: population size declined in almost all nodes in both seasons when compared with the control (the only exception was node B1, which experienced a small increase of 0.9%). However, these changes were only statistically significant for nodes B2 ($\beta = -30.505$, SE = 11.333, $t = -2.692$, $P = 0.015$, $R^2 = 0.27$), NB1 ($\beta = -59.137$, SE = 8.081, $t = -7.318$, $P = 0.001$, $R^2 = 0.49$) and NB2 ($\beta = -14.805$, SE = 5.806, $t = -2.550$, $P = 0.020$, $R^2 = 0.30$) with a decline in population size of 13, 38 and 8% respectively (Table S9). Because there was no mixing of individuals across nodes between seasons in the disconnected network (Fig. 1b), habitat loss caused a decline in population size only in nodes B1 (20%; $\beta = -52.242$, SE = 17.086, $t = -3.058$, $P = 0.007$, $R^2 = 0.30$) and NB1 (39%; $\beta = -66.116$, SE = 9.476, $t = -6.977$, $P < 0.001$, $R^2 = 0.42$) when compared to population size in the control replicates (Table S10). The results from the model also partially supported the *knock-on-effect hypothesis*: in the connected network, there was a decline in population size in all breeding nodes (9, 4 and 1% for nodes B1, B2 and B3 respectively). In the non-breeding nodes, although sites NB2 and

NB3 experienced an increase in population size, these values were very small (4 and 1% respectively; Figs 2e and 2f and Fig. S1). In the disconnected network, habitat loss only affected sites B1 and NB1 (a decline of 20 and 52% respectively).

Contrary to the *buffer hypothesis*, we did not find a significant difference in global population size in the habitat loss replicates between connected and disconnected network when population size was assessed either at the end of the breeding season (6% of decline in global population size in both types of network; $\beta = 21.813$, SE = 16.154, $z = 1.350$, $P = 0.178$, $R^2 = 0.15$; Table S11) or at the end of the non-breeding season (10 and 16% of decline in global population size in the connected and disconnected network respectively; $\beta = -14.288$, SE = 10.558, $z = -1.353$, $P = 0.176$, $R^2 = 0.35$; Table S11). The results from the model showed a similar decline in population size in both types of network: the decline in breeding population size was 5 and 7% for the connected and disconnected network respectively. For the non-breeding season, the population declined 16% in both types of networks.

Table 1 Parameters obtained from GLMMs to explain variation in population size by the end of the breeding season in different migratory routes (or edges) for the connected network

Edge	Parameter	Estimate	SE	z	P	R²	C	HL	%
B1 → NB1	Treatment × Generation	−0.007	0.036	−0.200	0.941	**0.32**			
	Treatment	**−0.190**	**0.064**	**−2.970**	**0.003**		**215.92**	**178.57**	**−21**
B2 → NB2	Treatment × Generation	0.015	0.027	0.560	0.577	0.45			
	Treatment	−0.023	0.046	−0.490	0.625		226.65	213.49	−6
B3 → NB3	Treatment × Generation	0.041	0.042	0.970	0.467	0.31			
	Treatment	−0.023	0.04604	−0.490	0.625		241.72	238.89	−1
B1 → NB2	Treatment × Generation	**0.271**	**0.131**	**2.070**	**0.038**	**0.74**			
	Treatment	0.998	0.310	3.218	0.001		**29.32**	**57.31**	**49**
B2 → NB1	Treatment × Generation	0.152	0.198	0.770	0.441	**0.74**			
	Treatment	**−0.891**	**0.347**	**−2.564**	**0.010**		**31.36**	**14.73**	**−113**
B2 → NB3	Treatment × Generation	0.188	0.300	0.627	0.530	0.85			
	Treatment	−0.244	0.506	−0.482	0.630		27.09	31.94	15
B3 → NB2	Treatment × Generation	**−0.366**	**0.166**	**−2.211**	**0.027**	**0.85**			
	Treatment	−0.718	0.338	−2.124	0.034		**24.97**	**15.63**	**−60**
B1 → NB3	Treatment × Generation	0.117	0.182	0.642	0.521	0.64			
	Treatment	−0.011	0.289	−0.039	0.969		3.97	4.12	4
B3 → NB1	Treatment × Generation	−0.055	0.377	−0.145	0.885	0.86			
	Treatment	−0.597	0.450	−1.327	0.185		4.00	1.59	−152

Only estimates for the effect of the interaction between treatment and generation and the effect of treatment are shown (see Table S7 for details of the model results). Control (C) and HL (Habitat loss) represent mean value of population size at the end of the breeding season for control and habitat loss replicates respectively. We also report the percentage difference (%) between C and HL; negative values indicate that population was smaller in the habitat loss treatments compared to the control. Edges in bold indicate that either the interaction between treatment and generation or the effect of treatment was statistically significant ($P < 0.05$).

DISCUSSION

The effects of environmental stressors on the population dynamics of mobile organisms are difficult to predict because vital rates can be influenced by events that take place at different periods of an animal's life cycle. Here, we used a unique experimental approach to test predictions about the effects of habitat loss on the dynamics of migratory networks. As predicted by the *mixing hypothesis*, habitat loss at a single non-breeding node caused population size to decline in edges that were both directly and indirectly connected to the node where habitat loss happened, but increased population size in edges that were directly connected to the breeding node closest to where habitat loss happened (Sutherland & Dolman 1994; Dolman & Sutherland 1995; Taylor & Norris 2010). The good match between our empirical results using fruit flies and results from theoretical models (e.g. Taylor & Norris 2010) suggests that predictions from the *mixing hypothesis* are fairly robust and could, therefore, be applicable to a wide range of species. Our results provide the first empirical support that differences in quality between sites or nodes within a season is the primary cause for variation in the degree of connectivity within a migratory network. This is consistent with the observation that heterogeneity in carrying capacity among sites is the norm rather than an exception in natural populations and explains why connected networks are predominantly found in nature (Boulet et al. 2006; Norris et al. 2006; Flockhart et al. 2015; Kennedy et al. 2013).

We also found that perturbation in a single node in a connected network had effects on other nodes throughout the network, even if migrating individuals were not directly connect to that node. Consistent with the *knock-on effect hypothesis*, nodes closest to the node in which habitat loss occurred were most influenced by habitat loss. However, the direction of such effects was not always consistent with the *knock-on effect hypothesis*. Unlike theoretical models (Taylor & Norris 2010), our experimental results provide little evidence for a decrease in population size in the breeding nodes, and the non-breeding nodes experienced a decrease, not an increase, in population size. The lack of support for these predictions could be related to reproductive potential. In the first two generations after habitat loss, populations in each edge sharply declined. However, population size tended to quickly recover (e.g. see edge B1 → NB1 in Fig. 2b), likely because fruit flies have such high reproductive rates. With a high number of individuals moving to the non-breeding sites, strong density-dependent effects on survival was likely the primary reason that kept population size at comparable levels to the control. Thus, it is likely that understanding the specific dynamics of migratory networks will partly depend on how resilient species are to perturbation, which is often linked to their life history (Sibly et al. 2007).

Our results did not provide strong support for the *buffer hypothesis*, and it is possible that connected networks only buffer global populations from decline at higher levels of habitat loss. Taylor & Norris (2010) found theoretical support for the buffer hypothesis at 80% habitat loss at a single node compared to 30% in our experiment. Higher levels of habitat loss could result in a greater degree of connectivity by creating relatively more incentive for individuals to populate edges originating from more distance nodes. A more connected network should be better able to dampen the loss incurred at a single node. To test this, we simulated 60 and 80% of habitat loss in both a connected and disconnected network (see Supporting information for details). Consistent with this hypothesis, global population size in the disconnected network was 7 and 12% for 60 and 80% levels of habitat loss, but only 5
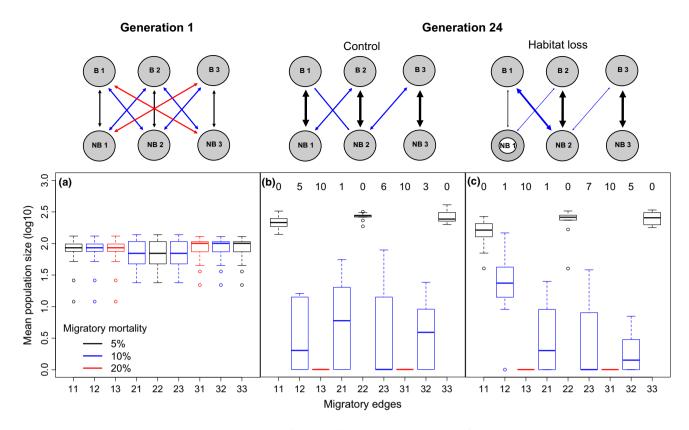
Figure 3 Box plot with mean population size ($\log_{10}$) at the end of the breeding season at generation 1 for the control (a; $n = 10$) and at generation 24 for both the control (b; $n = 10$) and habitat loss treatment (c; $n = 10$) treatments. Schematic networks at the top of each boxplot represent the configuration of the habitat loss for most of the replicates at generation 1 (a) or 24 (b, c; edges shown if they were in more than 50% of the replicates). Edge numbers indicate the direction of movement from the breeding to the non-breeding season (see text for details). Numbers at the top of each migratory edge in (b) and (c) represent the number of edges that went extinct after 24 generations. We added 1 to the raw data before log transformation so that when mean of population size ($\log_{10}$) is equal 0, all replicates went extinct.

and 6% for the connected network respectively (see Supporting information for details). Thus, connected networks may only buffer global populations from decline when either the level of habitat loss at a single node is relatively high (e.g. > 60%) or, analogously, when there is strong heterogeneity among nodes within the network.

We provide the first experimental system to examine the dynamics of populations in migratory networks. Although highly artificial, we believe that our simple design captured the general characteristics of most migratory systems whereby individuals are distributed over a series of interconnected breeding and non-breeding sites and the movement of those individuals across seasons causes sites to be demographically linked (Fancy et al. 1989; Webster et al. 2002; Taylor & Norris 2010; Allen et al. 2013; Kennedy et al. 2013; Flockhart et al. 2015). One criticism of our experimental system may be that ratio of time flies spend during the non-breeding period vs. the breeding period (4 days vs. 18 days respectively) does not capture a typical ratio that is found in nature. However, it is important to note that 16 days of the breeding season are actually devoted to the development from eggs to larvae and 1 day is for flies to clean themselves. Thus, the actual time adults get to breed is just 1 day or 25% of the total time they spend in the non-breeding vials, which mimics the ratio of time spent between breeding and non-breeding periods in many migratory species.

One of the advantages of our experimental system is that it can be adapted to accommodate many other features of natural migratory networks. For example many migratory species use stopover sites to refuel during migration and the quality of these sites can influence breeding and survival (Sawyer & Kauffman 2011). Furthermore, a single stopover site could be used by a relatively large number of breeding or non-breeding populations (e.g. Laughlin et al. 2013) so changes in the quality of such stopover sites would presumably have wide-ranging effects within the network. This situation could be easily created in our system by introducing another series of 'habitats' with smaller carry-capacities that are used between the breeding and non-breeding periods for shorter periods of time. It would also be possible to simulate multi-generational annual cycles, such as those found in migratory monarch butterflies (Flockhart et al. 2015), by simply having a series of breeding habitats prior to the commencement of the non-breeding period. It is also important note that, although our experimental system can accommodate most migration scenarios, it does not replicate movement processes. Thus, our results should be treated with caution because many of the complexities of movement are likely important for understanding the dynamics of migratory populations in the wild. We are currently working on developing a system that incorporates non-directed movements between seasons.

Understanding population dynamics of migratory animals is challenging because of their complex distribution over both space and time (Webster *et al.* 2002; Taylor & Norris 2010; Wiederholt *et al.* 2013). Our results demonstrate the important of understanding patterns of connectivity throughout a species range because these patterns may produce vastly different dynamics in response to environmental change. Predicting these effects is critical because there is a growing body of empirical evidence suggesting that migratory animals are highly vulnerable to environmental change (Wilcove & Wikelski 2008; Bowlin *et al.* 2010; Iwamura *et al.* 2013). Moreover, by travelling through different countries and even continents, migratory animals are potential vectors of infectious diseases, pests, and invasive species (Bauer & Hoye 2014). Our work helps to address fundamental aspects of how migratory networks are expected to respond to perturbations, which is essential for developing effective conservation plans (Martin *et al.* 2007), particularly since comprehensive demographic information on populations and migratory routes within a network is usually scarce or incomplete.

AUTHORSHIP

GSB, MJF and DRN designed the experiment; GSB conducted the experiments, analyses and simulations with assistance from DRN; GSB and DRN wrote the manuscript; DRN funded the project. All authors commented on the manuscript.

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