Demographic signals of population decline and time to extinction in a seasonal, density-dependent model

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Abstract

Nearly all wild populations live in seasonal environments in which they experience regular fluctuations in environmental conditions that drive population dynamics. Recent empirical evidence from experimental populations of *Drosophila* suggests that demographic signals inherent in the counts of seasonal populations, including reproduction and survival, can indicate when in the annual cycle habitat loss occurred. However, it remains unclear whether these signatures of season-specific decline are detectable under a wider range of demographic conditions and rates of habitat loss. Here, we use a bi-seasonal Ricker model to examine season-specific signals of population decline induced by different rates of habitat loss in the breeding or non-breeding season and different strengths of density dependence. Consistent with the findings in *Drosophila*, breeding habitat loss was accompanied by reduced reproductive output and a density-dependent increase in survival during the subsequent non-breeding period. Non-breeding habitat loss resulted in reduced non-breeding survival and a density-dependent increase in reproduction in the following breeding season. These season-specific demographic signals of decline were present under a wide range of habitat loss rates (2-25% per generation) and different density-dependent regimes (weak, moderate, and strong). We show that stronger density dependence can negatively influence time to extinction when non-breeding habitat is lost, whereas the strength of density dependence does not influence time to extinction with breeding habitat loss (although, in all cases, density dependence itself was an important modulator of population dynamics). Our results illustrate the need to incorporate seasonality in theoretical models to better understand when populations are being driven to decline.

Keywords: bi-seasonal, breeding, carrying capacity, density dependence, extinction, non-breeding, Ricker model, vital rates

Introduction

Habitat loss and fragmentation due to human land-use, have been identified as the leading causes of decline in wild populations observed in recent decades (Pimm et al. 2014; Díaz et al. 2019; but see Fahrig 2003, 2019). Habitat deterioration is the primary risk to approximately 30 percent of threatened species and one of the major threats to 85 percent of all species identified on the IUCN's Red List (World Wildlife Fund 2018; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2019). An understanding of not only what environmental factors are driving these populations to extinction, but also when and where these forces play out within the annual cycle, is imperative to global conservation efforts. Simple demographic models provide a theoretical underpinning to our understanding of the dynamics of natural systems, and represent an important tool in our arsenal for characterizing, managing, and conserving threatened populations (Beissinger and Westphal 1998; Gimona 1999; Norris 2004; García-Díaz et al. 2019).

Climatic seasonality is a fundamental component of natural environments, driving the regular fluctuations in resource availability and quality to which most species and populations are subjected. And yet, early models of population growth, such as the logistic growth curve (Verhulst 1845; Pearl and Reed 1920) and the Ricker model (Ricker 1954) did not explicitly incorporate the potential for seasonal dependence, and the population dynamical implications of seasonality are generally underappreciated (White and Hastings 2020). Despite their simplicity, these models can still offer important insights into fundamental ecological processes that underpin the dynamics of a wide range of natural systems (Ricker 1963; Borlestean et al. 2015; Romero et al. 2017; Bolser et al. 2018). Although population models are still frequently framed around a stationary, or 'aseasonal', context (Ludwig 1996; Mueller and Joshi 2000; Lande et al. 2003; Otso and Meerson 2010), explicit incorporation of the impacts of seasonality on population dynamics has proven fruitful (Skellam 1967; Fretwell 1972; Kot and Schaffer 1984; Sutherland 1996; Norris 2005; Liz 2017).

Despite lacking explicit seasonality, the strength of simple population models like the logistic and Ricker models is that they capture the important role of density dependence in explaining fluctuations in abundance over time. Density-dependent mechanisms arise when the rate of population growth (or change) at any given time is, at least in part, contingent on the current population density (Hassell 1986). The strength of density dependence is expected to

93 modulate the effects of habitat loss and impact population responses to environmental change
94 (Sutherland 1996; Agrawal et al. 2004; Norris 2005). Sequential density dependence, through
95 which population abundance in one season influences population vital rates in the next (Norris
96 2005; Ratikainen et al. 2007; Betini et al. 2013a), may affect the capacity for populations to
97 respond to environmental change, and may also result in different system dynamics in those
98 losing breeding or non-breeding habitat. While aseasonal models generally capture density
99 dependence in population growth rate (r), seasonal models allow the decomposition of density-
100 dependent effects in the different periods (i.e., in a bi-seasonal model, we can now model two
101 growth rates, r_b in the breeding period and r_{nb} in the non-breeding period). In a series of studies,
102 Betini et al. (2013a, 2013b, 2014) demonstrated how density dependence acts to regulate
103 seasonal population dynamics in an experimental population of *Drosophila melanogaster* with
104 distinct breeding and non-breeding periods.
105 In a recent experimental study, we investigated how seasonal changes in habitat
106 availability influenced the dynamics of the same seasonal *Drosophila* populations, and found
107 that populations losing breeding versus non-breeding habitat responded in the different ways
108 (Burant et al. 2019). In the experiment, seasonality was induced by manipulating the quality food
109 provided (Betini et al. 2013b) and chronic, season-specific habitat loss was imposed over
110 multiple generations by systematically reducing the volume of food provide in one period while
111 holding it constant in the other (Burant et al. 2021). The loss of breeding habitat resulted in a
112 decline in *per capita* reproduction and, as a consequence of fewer individuals entering the
113 subsequent non-breeding period, an increase in non-breeding survival via positive sequential
114 density dependence. Conversely, loss of non-breeding habitat had the opposite effect: non-
115 breeding survival declined due to resource limitation, while *per capita* reproduction showed an
116 increase in the subsequent breeding period via positive sequential density dependence (Burant et
117 al. 2019). Moreover, we demonstrated that simple demographic and statistical signals derived
118 from population counts and vital rates, including non-breeding survival, reproduction and other
119 statistical indicators inherent in time series of population abundance, can be used to identify the
120 season in which habitat loss occurred (Burant et al. 2019). However, the experiment only
121 considered two different rates of breeding or non-breeding habitat loss (10% and 20% per
122 generation) and was conducted under levels of breeding and non-breeding density dependence
123 characteristic of a specific, laboratory-evolved strain of *Drosophila*. Thus, the extent to which

these empirical results are relevant for other populations under a broader range of strengths of density dependence and rates of habitat loss remains unclear.

In this study, we use a bi-seasonal Ricker model (Betini et al. 2013a) to explore how different rates of habitat loss in either the breeding or non-breeding period and the strength density dependence influence the production of simple, season-specific signals of population decline and time to extinction *in silico*. The original (aseasonal) Ricker model was developed in the context of fisheries harvesting (Ricker 1954) and has since been extended for application in a variety of contexts, modelling the population dynamics for a broad range of taxa, including fishes (e.g., Myers et al. 1999), crustaceans (e.g., Twombly et al. 2007), and insects (e.g., Dey and Joshi 2006; Estay et al. 2009). Here, we incorporate the effects of season-specific habitat loss on carrying capacity and growth in each period of the bi-seasonal model, and use simulations to explore how habitat loss operates under a range of initial parameter values, strengths of density dependence, and rates of seasonal habitat loss. We derive season-specific vital rates (survival and reproduction) to look at sequential density-dependence between periods of breeding and non-breeding (Betini et al. 2013a), rather than density dependence in population growth between generations.

Given the discrete nature of our model, with breeding and non-breeding conditions modelled as two separate equations and resource pools (habitats), we expect that this model may be particularly relevant for migratory species (e.g., migratory birds) that occupy distinct breeding and non-breeding habitats. For example, our model captures the plausible scenario in which a population experiences habitat loss (or another environmental forcing) on the breeding grounds, while the non-breeding sites remain relatively stable (or *vice versa*). However, even in resident species that occupy the same habitat throughout the year, populations may experience differential changes in resource availability and quality during periods of breeding and non-breeding, which may impact their overall dynamics in a similar way. Thus, the model we present and others that explicitly incorporate seasonality (White and Hastings 2020) have a broad scope of application.

Methods

Bi-seasonal Ricker model with season-specific habitat loss

The Ricker model (eq. 1) was first introduced by W.E. Ricker (1954) in the context of fisheries management, following his observation that the convex relationship between net reproduction and population density resulted in oscillations in population abundance. Since then, the Ricker model has become one of the classical theoretic models to describe density-dependent dynamics in populations with discrete time intervals (Fretwell 1972; Kot and Schaffer 1984; Turchin 2003; Geritz and Kisdi 2004; Wysham and Hastings 2008). The Ricker model can be expressed as:

$$N_{(t+1)} = N_{(t)} e^{r\left(1-\frac{N_{(t)}}{K}\right)} \quad \text{(eq. 1)}$$

where N represents the number of individuals in the population at a given time t, r is the intrinsic growth rate ('Malthusian parameter'; Fisher 1930), and K indicates a population's carrying capacity (Pearl and Reed 1920). The simple Ricker model has been used previously to model the population dynamics of *Drosophila* (Mueller and Joshi 2000; Dey and Joshi 2006). This aseasonal model results in stable population cycles for a range of r and K, which can be either arbitrary or empirically defined, but generates chaotic dynamics when r is large (r > ~2.7; May and Oster 1976; May 1987). Griffen and Drake (2008) showed that reductions in habitat quality produced reductions in both r and K, as modelled for experimental populations of the water flea *Daphnia magna*.

To investigate the dynamics of *D. melanogaster* with distinct breeding and non-breeding periods, Betini et al. (2013a) extended the Ricker model to include season-specific parameters for population growth and carry capacity. For this 'seasonal' Ricker model, temporal changes in breeding (N_b) and non-breeding (N_{nb}) population abundance can be modelled using a set of two interacting equations (eq. 2.1, 2.2). For each generation, population size at the beginning of the non-breeding period (i.e., the number of offspring produced; maximum population size in a given generation) can be written as the difference equation:

$$N_{nb(t+1)} = N_{b(t)} e^{r_b\left(1-\frac{N_{b(t)}}{K_b}\right)} \quad \text{(eq. 2.1)}$$

where r_b and K_b are the maximum growth rate (reproduction) and carrying capacity for the breeding period, b, respectively. In this way, nonbreeding, nb, population size (N_{nb}) is a product of the number of breeders (N_b) and density-dependent interactions between them (Betini et al.

178 2013a, 2013b). Population size at the beginning of the breeding period (i.e., the number of
179 potentially breeding adults that survived the previous non-breeding period) can be described as:

$$N_{b(t+1)} = N_{nb(t+1)} e^{r_{nb}\left(1-\frac{N_{nb(t+1)}}{K_{nb}}\right)} \quad \text{(eq. 2.2)}$$

180 where r_{nb} and K_{nb} are the maximum growth rate (mortality) and carrying capacity for the non-
181 breeding period, respectively.

182 In this study, we were interested in modelling the impacts of chronic, season-specific
183 habitat loss on the predicted changes in breeding and non-breeding population size under a range
184 of conditions. In a previous experiment (Burant et al. 2019), we systemically reduced the amount
185 of food provided to replicate populations of *Drosophila* in either the breeding or non-breeding
186 period over multiple generations, until the populations went extinct. In our experiment, and in
187 the theoretical model presented here, season-specific habitat loss followed an exponential decay,
188 with the proportion of food provisioned in the season of habitat loss in a particular generation
189 $H_{(t)}$ prescribed as:

$$H_{(t)} = (1 - v)^t \quad \text{(eq. 3)}$$

190 *w*here v is the rate of habitat loss and *t* is the number of generations since habitat loss treatment
191 commenced.

192 In an attempt to replicate the experimental reductions in habitat, we represented habitat
193 loss by altering season-specific *r* and *K* parameters. Given that both population growth rate and
194 carrying capacity have been shown to be dependent on the quantity of food provisioned (Griffen
195 and Drake 2008), we scaled both parameter values proportionally with the rate of habitat loss.
196 For populations losing breeding habitat, our model assumed that both r_b and K_b would decrease
197 proportionally with the rate of habitat loss (eq. 4.1), such that the total number of offspring
198 produced by the previous generation $N_{nb(t+1)}$ would also decrease. Changes in population growth
199 rates and carrying capacities with breeding habitat loss can be summarized as:

$$K_{b(t)} = K_b^* H_{b(t)} \quad \text{(eq. 4.1)}$$

$$r_{b(t)} = r_b^* - r_b^*\left(1 - H_{b(t)}\right) = r_b^* H_{b(t)}$$

$$K_{nb(t)} = K_{nb}^*$$

$$r_{nb(t)} = r_{nb}^{*}$$

where K_b^* and r_b^* are the estimated carrying capacity and intrinsic growth rate during the breeding period under control (no habitat loss) conditions, respectively, K_{nb}^* and r_{nb}^* are the corresponding non-breeding values, and $H_{b(t)}$ is the proportion of breeding habitat remaining.

For populations losing non-breeding habitat, we expected the opposite effects on season-specific growth rates and carrying capacities. We predicted that K_{nb} would decrease proportionally to the rate of habitat loss and r_{nb} would become more negative (increasing mortality) as the proportion of habitat remaining continued to decline (eq. 4.2). Changes in population growth rates and carrying capacities with non-breeding habitat loss can be summarized as:

$$K_{b(t)} = K_b^{*} \qquad \text{(eq. 4.2)}$$

$$r_{b(t)} = r_b^{*}$$

$$K_{nb(t)} = K_{nb}^{*} H_{nb(t)}$$

$$r_{nb(t)} = r_{nb}^{*} - |r_{nb}^{*}|\left(1 - H_{nb(t)}\right)$$

where $H_{nb(t)}$ is the proportion of non-breeding habitat remaining. Scaling the season-specific growth rates and carrying capacities in this way had the effect of holding the strength of density dependence (see below) constant in the season of habitat loss.

Model simulations

To explore the dynamics of our bi-seasonal Ricker model with season-specific habitat loss, we first parameterized the model using estimates derived from a set of input-output experiments in seasonal populations of *Drosophila* (Betini et al. 2013a). In these trials, populations of breeding and non-breeding fruit flies were initiated at a range of densities, and their subsequent reproductive output (breeding) and survival (non-breeding) were measured. The experimental density dependence reference parameters from Betini et al. (2013a) were: $r_b = 2.24$, $\alpha_b = 9.86 \times 10^{-3}$, $r_{nb} = -0.0568$, and $\alpha_{nb} = 6.72 \times 10^{-4}$, where α describes the strength of density dependence in an alternative form of the Ricker model and can be calculated as $\alpha_i = r_i / K_i$ (see *Supplementary Information* for results of model parameterization with empirical values; Fig. S3).

To investigate how the strength of density dependence influenced the trajectories of populations and the production of seasonal signals of decline, we further explored three other parameterizations in which the strength of density dependence was manipulated by changing the value of r (in the same direction) in both seasons: (1) weak density dependence (r_b = 1.3, r_{nb} = -0.033); moderate density dependence (r_b = 2, r_{nb} = -0.051); strong density dependence (r_b = 2.65, r_{nb} = -0.069). These values of r_b are selected somewhat arbitrarily to sample the range of the non-zero equilibrium, non-chaotic phase of the Ricker model (r < 1 results in populations shrinking to zero; chaotic dynamics set in at $r \approx 2.7$). The corresponding r_{nb} values are matched based on the ratio of the experimentally-derived parameters (e.g., $r_{nb(moderate)} = r_{nb(experimental)}$ x 2 / 2.24). This manipulation of r is consistent with previous experimental work, which has shown that, intuitively, maximum growth rates may be useful as a predictor of the strength of density dependence in systems that conform to the monotonic definition of density dependence inherent in most simple population models (Agrawal et al. 2004). Because carrying capacity is largely a function of the volume of food provided (e.g., Griffen and Blake 2018; Burant et al. 2020), and not the strength of density dependence, the season-specific carrying capacities (K_b = 227, K_{nb} = -84.5) were the same for all three theoretical scenarios and the initial empirical parameterization.

To simulate some degree of variability in the baseline parameters, which should be expected for real world replicate populations, we treated these parameters as normal distributions $N(\mu, \sigma^2)$ from which the initial values K_b^*, r_b^*, K_{nb}^*, and r_{nb}^* could be sampled. For the season-specific carrying capacities, the standard deviation of K_i was set as $\sqrt{|K_i|}$. Since the square-root of a value < 1 is larger than the initial value, the standard deviation for the season-specific growth rates r_i was set as r_i /10.

We simulated a range of rates of season-specific habitat loss, with populations losing habitat at a rate of 2%, 5%, 10%, 20%, or 25% per generation in either the breeding or the non-breeding period. We also included control simulations, in which habitat availability was constant in both seasons. As with our experiment, which included 10% and 20% rates of habitat loss (Burant et al. 2019), replicate simulations were initiated with a non-breeding population size of 20 individuals. We simulated 20 generations of 'pre-treatment' population growth in which the proportion of habitat provisioned in the treatment period remained at 100%. Starting in generation 21, the simulated proportion of habitat provisioned in the treatment period

252 corresponded to the rate of loss following eq. 3. We ran each model simulation for 50
253 generations (including the pre-treatment period), or until the population went extinct.
254 For each strength of density dependence scenario, we performed 1,000 model simulations
255 for different rate of loss and season of loss combinations (e.g., 2% breeding, 2% non-breeding,
256 5% breeding, etc.), with 10 rate-by-season treatment combinations plus controls. In order to
257 avoid overfitting our statistical models (see *Supplementary Information*), and to introduce an
258 additional degree of randomness in the initial parameter values that were used to specify each
259 run, we randomly sampled 25 of the 1,000 simulations for each treatment for analysis.
260 From each replicate, we derived time series of the following metrics: (1) *breeding*
261 *abundance* (i.e., the number of potential breeders, the number of individuals at the end of the
262 non-breeding period); (2) *non-breeding abundance* (i.e., the number of offspring produced, the
263 number of individuals at the start of the non-breeding period); (3) *per capita reproduction* (i.e.,
264 the relative change in abundance between the beginning and end of the breeding period, non-
265 breeding abundance / breeding abundance); and (4) *non-breeding survival* (i.e., the relative
266 change in abundance between the beginning and end of the non-breeding period, breeding
267 abundance / non-breeding abundance). Time to extinction was calculated as the number of
268 generations from the initiation of habitat loss (i.e., generation – 20) until abundance ≤ 2
269 individuals in the breeding period.

270 *Relative strength of density dependence*
271 To explore the density-dependent nature of time to extinction that we identified in our model
272 simulations of non-breeding habitat loss, we systemically varied the strength of density
273 dependence in either the breeding and non-breeding period independently while holding density
274 dependence constant (moderate) in the other season. As with all parameterizations, the relative
275 strength of density dependence was always higher in the breeding period ($\alpha_{weak} = 5.73 \times 10^{-3}$,
276 $\alpha_{moderate} = 8.81 \times 10^{-3}$, $\alpha_{strong} = 1.17 \times 10^{-2}$) than that in non-breeding period ($\alpha_{weak} = 3.91 \times 10^{-4}$,
277 $\alpha_{moderate} = 6.00 \times 10^{-4}$, $\alpha_{strong} = 8.11 \times 10^{-4}$; see *Model simulations*). Extinction time was
278 determined by performing a single iteration of the non-breeding habitat loss model with each
279 combination of breeding and non-breeding strengths of density dependence.

The theoretical model was constructed in the R statistical environment (v. 4.0.2; R Core Team 2020). The code and data used in these analyses have been made publicly available (Burant and Norris 2022).

Results

Bi-seasonal population dynamics with habitat loss

Simulations of a bi-seasonal Ricker model with season-specific habitat loss (see *Model simulations* in *Methods*) produced two counts in each generation (breeding abundance and non-breeding abundance), with distinct dynamics that varied with the season and rate of habitat loss (Fig. 1). In the initial pre-treatment generations, during which all replicate populations were allowed to grow from an initial non-breeding population size of 20 individuals, all treatment scenarios showed a rapid increase towards carrying capacity and stable seasonal oscillations in the generations preceding the introduction of treatment. For control replicates, in which habitat availability remained constant in both the breeding and non-breeding period, population abundances in both seasons were stable throughout the treatment period. Control breeding abundance was largely similar across the different strengths of density dependence (mean breeding abundance: weak DD = 206 ± 2.48 (mean ± SE); moderate DD = 200 ± 3.89; strong DD = 199 ± 2.51; Fig 1a, d, g; Fig. S1). In contrast, control non-breeding abundance increased with the strength of density dependence (mean non-breeding abundance: weak DD = 233 ± 3.20; moderate DD = 247 ± 5.54; strong DD = 276 ± 26.5; Fig. 1a, d, g; Fig. S2). Between-season variability in abundances increased with stronger density dependence (Fig. 1).

With reductions in breeding habitat, there were similar patterns of decline in both breeding and non-breeding abundance, with declines in both seasons beginning within 1-2 generations of the onset of treatment (Fig. 1b, e, h; Fig. S1; Fig. S2). In contrast, when non-breeding habitat was lost, breeding and non-breeding population abundance appeared to diverge in simulations (Fig. 1c, f, i; Fig. S1; Fig. S2). Breeding population abundance declined steadily as non-breeding habitat was lost, whereas non-breeding population abundance remained relatively stable for several generations before declining rapidly. At lower rates of non-breeding habitat loss (2% and 5% per generation), non-breeding abundance actually increased slightly for several generations preceding the rapid decline (Fig. 1b, e, h; Fig. S2). The transition from high, stable non-breeding abundance to rapid decline occurs around generation 21, 16, 14, 12, and 11

for non-breeding habitat loss treatments of 2%, 5%, 10%, 20%, and 25% habitat loss per generation (Fig. S3).

Response of vital rates to season-specific habitat loss

As expected, breeding and non-breeding habitat loss generated distinct changes in population vital rates (Fig. 2; Fig. 3; *Supplementary Information*). For control replicates, *per capita* reproduction declined rapidly as populations grew towards carrying capacity in the pre-treatment period, and remained stable during the treatment generations (mean *per capita* reproduction = 1.13 ± 0.004, 1.28 ± 0.04, and 2.07 ± 0.40 offspring/breeder with weak, moderate, and strong density dependence, respectively; Fig. 2a, d, g). When breeding habitat was lost, *per capita* reproduction dropped and remained below one (i.e., the replacement value) as the amount of breeding habitat available in each generation continued to decline. *Per capita* reproduction shifted from being relatively stable in the generations preceding population collapse to zero within a single generation (Fig. 2b, e, h). In contrast, non-breeding habitat loss generated a steady increase in *per capita* reproduction, with values exceeding those observed for control simulations, as one might expect given the assumed pattern of compensatory density dependence (Fig. 2c, f, i). As the rate of non-breeding habitat loss increased, the relative increase in *per capita* reproduction decreased, likely as a result of reduced time available for simulations to respond to shifting conditions.

Non-breeding survival remained relatively high throughout the treatment period for control simulations (mean non-breeding survival = 88.4 ± 0.003%, 79.1 ± 0.006%, and 75.7 ± 0.02% for weak, moderate, and strong density dependence, respectively), and was as high as 100% in the initial generations of the pre-treatment period (Fig. 3a, d, g). When breeding habitat was lost, the proportion of individuals that survived the non-breeding period increased to one as the number of individuals entering the non-breeding period decreased (Fig. 3b, e, h). With non-breeding habitat loss, non-breeding survival decreased proportionally with the rate of habitat loss (Fig. 3c, f, i). Interestingly, all non-breeding habitat loss simulations reached a plateau around 20-25% non-breeding survival in later generations (i.e., when the volume of non-breeding habitat provisioned was low), with non-breeding survival actually increasing in the generation preceding population collapse, before declining to zero as the populations went extinct. This result may provide some

evidence for an Allee effect on survival with non-breeding habitat loss, likely because relatively few offspring are produced by breeders at very low densities.

Time to extinction

Season-specific habitat loss resulted in rapid changes in bi-seasonal population dynamics, with breeding and non-breeding habitat loss generating different patterns of population decline and timing of population collapse (Fig. 1b, c, e, f, h, i). As expected, the pace at which populations declined towards extinction increased with the rate of habitat loss. However, there was a notable difference between simulations of breeding and non-breeding habitat loss in the effect of the strength of density dependence on the timing of population collapse (Fig. 4). When breeding habitat was lost, the timing of population collapse appeared to be almost entirely dependent on the rate of habitat loss, with relatively little impact of the strength of density dependence imposed on the population (Fig. 4a). With breeding habitat loss, all replicate populations went extinct within 19, 11, 7, 4, and 3 generations with the onset of habitat loss treatments of 2%, 5%, 10%, 20%, and 25% loss per generation, respectively. In contrast, when non-breeding habitat was lost, the time to extinction was negatively related to the strength of density dependence (Fig. 4b), such that populations subjected to weak density dependence collapsed later than those subjected to strong density dependence. Across all scenarios, populations losing non-breeding habitat went extinct earlier than those losing breeding habitat (Fig. 1; Fig. 4; Fig. S3).

Because we varied the strength of density dependence simultaneously in both seasons, we were also interested in examining whether season-specific variation in density dependence could be driving the negative relationship between density dependence and time to extinction when non-breeding habitat was lost. To do this, for the non-breeding habitat loss scenarios, we varied the strength of density dependence in one period while holding the other at a moderate level, and then examined the time to extinction. When the strength of non-breeding density dependence was held at a moderate level and non-breeding habitat was lost, stronger breeding density dependence resulted in earlier population extinction (Fig. 5a), similar to the results reported above. In contrast, when breeding density dependence was held at a moderate level and non-breeding habitat was lost, variation in the strength of non-breeding density dependence had no impact on the timing of population collapse (Fig. 5b).

Discussion

We were interested in exploring whether season-specific signals of population decline observed in earlier experiments on seasonal populations of *Drosophila* (Burant et al. 2019) arise under a wider range of demographic conditions and rates of habitat loss. Several broad similarities in the overall patterns of decline from our experiment and theoretical model suggest that the latter does a reasonable job of approximating the former. First, while mean extinction times estimated from the model (see *Bi-seasonal population dynamics with habitat loss* in *Results*) were earlier than experimentally-induced collapses (average times to extinction with 10% and 20% habitat loss per generation were 14 and 7 generations for breeding treatments, and 14 and 8 generations for non-breeding treatments; Burant et al. 2019), the relative order in extinction of populations losing breeding and non-breeding habitat was consistent with experimental observations. Likewise, in both the experiment and the model presented here, non-breeding habitat loss produced large fluctuations between breeding and non-breeding population abundance (as a result of density-dependent reproduction), while breeding habitat loss resulted in consistent, directional decline (compare Fig. 1 herein with Figure 2 in Burant et al. (2019)). While seasonality has been explicitly incorporated in other theoretical approaches (reviewed in White and Hastings 2020), and the consequences of season-specific forcing for population dynamics have also been explored (e.g., Norris 2005), here we further show how season-specific vital rates can serve to indicate the season of decline.

Our theoretical results demonstrate the important role that the strength of density dependence plays in determining how populations decline with seasonal habitat loss. Based on our simulations, the timing of population collapse with habitat deterioration during the breeding period was almost entirely dependent on the rate at which habitat was lost, with no impact of changes in the strength of density dependence. In contrast, strong density dependence amplified the impacts of non-breeding habitat loss, such that increased density dependence resulted in steeper population declines and earlier extinctions. The difference in the influence of density dependence with season-specific habitat loss is consistent with our predictions, and is ultimately a reflection of differences in the capacity of populations to respond to habitat loss in either the breeding or non-breeding period. With non-breeding habitat loss, populations may experience a 'seasonal compensation effect' (Norris 2005) that results in increased reproduction in the subsequent breeding period. A similar compensatory effect should not necessarily be expected

with breeding habitat loss, since, by definition, populations cannot grow during the subsequent non-breeding period. Moreover, any seasonal compensation effect with breeding habitat loss is constrained by ceiling effects, since the proportion of individuals that survive the non-breeding period cannot exceed 100 percent. This conclusion was supported by an exploratory analysis in which we manipulated the strength of density dependence separately in each period, which showed that changing non-breeding density dependence did not affect time to extinction when breeding density dependence was moderate.

Inspection of the breeding and non-breeding population abundance time series revealed a number of important differences between our theoretical and experimental results (see *Supplementary Information*). First, while the relative (but not absolute) timing of collapse was consistent between the experiment and model (see above), the way in which these declines unfolded differed. Although experimental populations did not appear to respond immediately to breeding habitat loss, with population size remaining relatively stable for several generations before declining precipitously (largely due to stable breeding abundances resulting from the strong filter of the non-breeding period; Burant et al. 2019), our theoretical model generated steady declines in abundance in both seasons with the onset of breeding habitat loss. Non-breeding habitat loss had similar effects on seasonal abundances, with delayed declines in non-breeding population size relative to breeding (as a result of density-dependent reproduction; Burant et al. 2019). Despite the fact that the control conditions in the experimental seasonal *Drosophila* system were empirically derived (G.S. Betini and D.R.N., *unpublished data*), it is possible that initial breeding food availability in our experiments was in excess of what was required to maintain stable bi-seasonal dynamics. This could have resulted in a delayed population response to reductions in breeding habitat. Moreover, carrying capacity in either season is not solely a function of the volume of food provided, since there is only so much space the flies can occupy in a closed system, and so there is the potential for overcrowding (rather than absolute food availability) to limit food access and ultimately affect differences in survival and reproduction (Burant et al. 2020; Kilgour et al. 2020). The potential for overcrowding was not accounted for in our theoretical model, and so changes in carrying capacity were assumed to be simply a function of food availability (see *Methods*). As a consequence of these intricacies, relative to our experiment (Burant et al. 2019), the simple theoretical model generally

underestimated breeding and non-breeding population abundance with breeding habitat loss, and overestimated breeding abundance when non-breeding habitat was lost.

We noted that, for non-breeding habitat loss simulations, non-breeding survival appeared to temporarily plateau in later generations when little non-breeding habitat remains and, in some instances, briefly increased in the generation preceding extinction (Fig. 3c, f, i). While not specifically encoded in the model, this is reminiscent of an Allee effect (Allee 1927; Stephens et al. 1999) in which population growth is limited at low breeding densities. In essence, low non-breeding habitat availability means only a few individuals survive to the next breeding period and, as a result, reproductive output and population growth are reduced due to low densities. In turn, only a few individuals enter the subsequent non-breeding period, where habitat availability continues to decline. Thus, non-breeding densities may be better matched to habitat availability than in previous generations when non-breeding survival declined rapidly due to the breeding season density-dependent, rebound-induced mismatch between the number of individuals entering the non-breeding period and the declining habitat availability. This plateau means populations persist longer than might otherwise be anticipated based on the steep decline in non-breeding survival observed at earlier timepoints. Why this arises in our model is not necessarily intuitive, but is possibly a product of the interplay between the density-dependent r_b (stable) and r_{nb} (increasingly negative). Allee effects have been explicitly incorporated in other modifications of the Ricker model (Elaydi and Sacker 2009), including the periodic Ricker map (Sacker 2006).

There are several other potential explanations for discrepancies between our previous observational results and theoretical outcomes. Betini et al. (2013a) showed that sequential density dependence and carry-over effects between seasons can influence reproductive output and regulate population abundance. However, fluctuations in population density and food availability between seasons are also expected to influence other aspects of individual and population performance, which may help to buffer populations against deteriorating environmental conditions. For example, reproductive output is known to be influenced by individual body condition, such that individuals who enter the breeding period in poor condition produce fewer offspring (Betini et al. 2014), and non-breeding food availability carries over to indirectly influence reproductive performance (Burant et al. 2020). These phenotypic traits, and their changes in response to seasonal variation, effectively link environmental conditions in one season with individual performance in the next (O'Connor et al. 2014). Similarly, interactions

among individuals in a population can be density-mediated, with individual behavioural expression modulated by social context (Sokolowski et al. 1997; Kilgour et al. 2018; Leatherbury and Travis 2019). Importantly, the impacts of density-dependent changes on population growth and individual traits are not necessarily immediately observable (Ratikainen et al. 2007). These are but a few examples of the mechanisms through which individuals and populations can respond to changing environmental conditions (Colchero et al. 2018). Although the purpose of simple population models is not necessarily to reproduce all possible mechanisms of change, discrepancies between our theoretical and empirical results demonstrate the importance of carry-over effects and other non-abundance traits that are expected to shift as the environment deteriorates. Indeed, recent theoretical work has demonstrated the importance of considering the impacts of seasonal carry-over effects on individual performance and, ultimately, how these effects scale up to influence population vital rates (e.g., Liz and Ruiz-Herrera 2016). Failure to fully consider carry-over effects is likely to limit our understanding of the dynamics of declining populations, and so also limit efforts to conserve them (O'Connor and Cooke 2015).

The present model is not the first to consider how seasonality shapes the dynamics of animal populations. Fretwell (1972) expounded at length about the various ways regularly varying environments influences individual reproduction and survival and, ultimately, population persistence. Others have considered the more general case of resource variability across different temporal scales (e.g., Hastings 2014). In its original formulation, the bi-seasonal Ricker model from Betini et al. (2013a) was important for demonstrating how explicit incorporation of density-mediated carry-over effects better captures long-term vital rate dynamics and population stability. The interplay between seasonality and stability was also explored by Kot and Schaffer (1984), who showed theoretically how moderate seasonality may stabilize populations in productive environments. Consistent with our findings, Kot and Schaffer (1984) also showed how increasing 'imbalance' between breeding and non-breeding seasons periods can have contrasting effects. Sutherland (1996) more explicitly considered the effects of season-specific habitat loss on the dynamics of migratory populations, and similarly found differential effects of breeding and non-breeding habitat loss. Although time to extinction was not directly evaluated, Sutherland (1996) showed that, compared to breeding habitat loss, the same amount of non-breeding habitat loss had more than twice the effect in terms of percent population decline. This is consistent with our finding that populations losing non-breeding habitat go extinct earlier than

491 those losing breeding habitat. Our analysis complements these previous studies by showing how
492 sequential density-dependent effects can modulate patterns of population decline and time to
493 extinction with chronic, season-specific forcing. By simulating habitat deterioration in one
494 season and holding it fixed in the other, we begin to explore how seasonal populations may be
495 temporarily buffered against decline through density-dependent survival and reproduction. In
496 addition, while we implement a seasonal formulation of the Ricker model, many other simple
497 demographic models exist and predictions from these models may differ from those presented
498 here. Previous comparison of the utility of different aseasonal models for predicting extinction in
499 a community context has shown that the strong density dependence inherent in the Ricker model
500 best matched results from simple microcosms (Ferguson and Ponciano 2013). Finally, although
501 we randomly sampled the initial values of r and K for the iterations of each scenario, our model
502 is strictly deterministic in that is does not incorporate a "noise" or error term, which may have
503 implications for the interpretation of the results. Indeed, previous work has shown that
504 incorporating demographic stochasticity can affect the reliability of extinction risk predictions
505 drawn from simple demographic models (e.g., Drake 2005).
506 Along with understanding the demographic mechanisms underlying patterns of
507 population decline, it is relevant to consider whether the predictability of collapse differs
508 between populations losing breeding and non-breeding habitat. In our chronic habitat loss
509 experiment, we showed that whether a set of indicators derived from time series of population
510 abundance (e.g., coefficient of variation, lag-1 autocorrelation) and fitness-related traits (e.g.,
511 body size, activity) served as early warning indicators of population collapse was dependent on
512 the season of habitat loss (Burant et al. 2021). Moreover, in a similar theoretical approach to the
513 one presented here, Bury (2020) showed that the nature of early warning signal production
514 differed between simulations of breeding and non-breeding habitat degradation. This theoretical
515 work also suggests the potential for using early warning indicators to identify the season in
516 which populations are being driving to decline, which we also previously demonstrated in our
517 experimental system (Burant et al. 2019). These results suggest that simple demographic vital
518 rates like survival and reproduction, as well as early warning indicators, may be useful for
519 detecting and predicting season-specific drivers of population decline across a wide range of
520 density-dependent systems.

In summary, the results from our theoretical model of the impacts of season-specific habitat loss on population dynamics through changes in growth and carrying capacity bolster our understanding of how populations decline in seasonal environments. By comparing our theoretical simulations to results from an earlier chronic habitat loss experiment, we are able to identify some of the ways in which simple population models can elegantly capture real-world phenomena. Along with experiments and observational studies, theoretical models represent an important tool, not only for understanding how the natural world works but particularly for efforts aimed at conserving threatened species in an era of rapid environmental change.

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Figure Captions

Figure 1. Population dynamics generated from a bi-seasonal Ricker model with season-specific habitat loss. Each generation is comprised of two counts: non-breeding population abundance (i.e., the number of individuals at the start of the non-breeding period; peaks), and breeding population abundance (i.e., the number of potential breeders at the start of the breeding period; troughs). The bi-seasonal time series includes two time-steps per generation. Replicate populations were simulated under control (no habitat loss conditions) for 20 generations while they grew toward carrying capacity (shaded grey region). In subsequent generations, season-specific habitat loss was simulated at 0% (control; a, d, g), 2%, 5%, 10%, 20%, or 25% per generation in either the breeding (b, e, h) or non-breeding period (c, f, i), under three different density dependence scenarios. (See *Model simulations* in *Methods*.) Sample size = 25 replicates per treatment.

Figure 2. Response of *per capita* reproduction to season-specific habitat loss with varying strengths of density dependence. In each generation, *per capita* reproduction was calculated as the number of offspring divided by the number of breeders. All replicates were simulated under control (no habitat loss conditions) for 20 generations while they grew toward carrying capacity (shaded grey region). In subsequent generations, season-specific habitat loss was simulated at 0% (control; a, d, g), 2%, 5%, 10%, 20%, or 25% per generation in either the breeding (b, e, h) or non-breeding period (c, f, i), under three different density dependence scenarios. (See *Model simulations* in *Methods*.) Sample size = 25 simulations per treatment.

Figure 3. Response of non-breeding survival to season-specific habitat with varying strengths of density dependence. In each generation, non-breeding survival was calculated as the number of individuals at the end of the non-breeding period divided by the number initial non-breeding abundance (i.e., the proportion of individuals who survived through the non-breeding period). All replicates were simulated under control (no habitat loss conditions) for 20 generations while they grew toward carrying capacity (shaded grey region). In subsequent generations, season-specific habitat loss was simulated at 0% (control; a, d, g), 2%, 5%, 10%, 20%, or 25% per generation in either the breeding (b, e, h) or non-breeding period (c, f, i), under three different

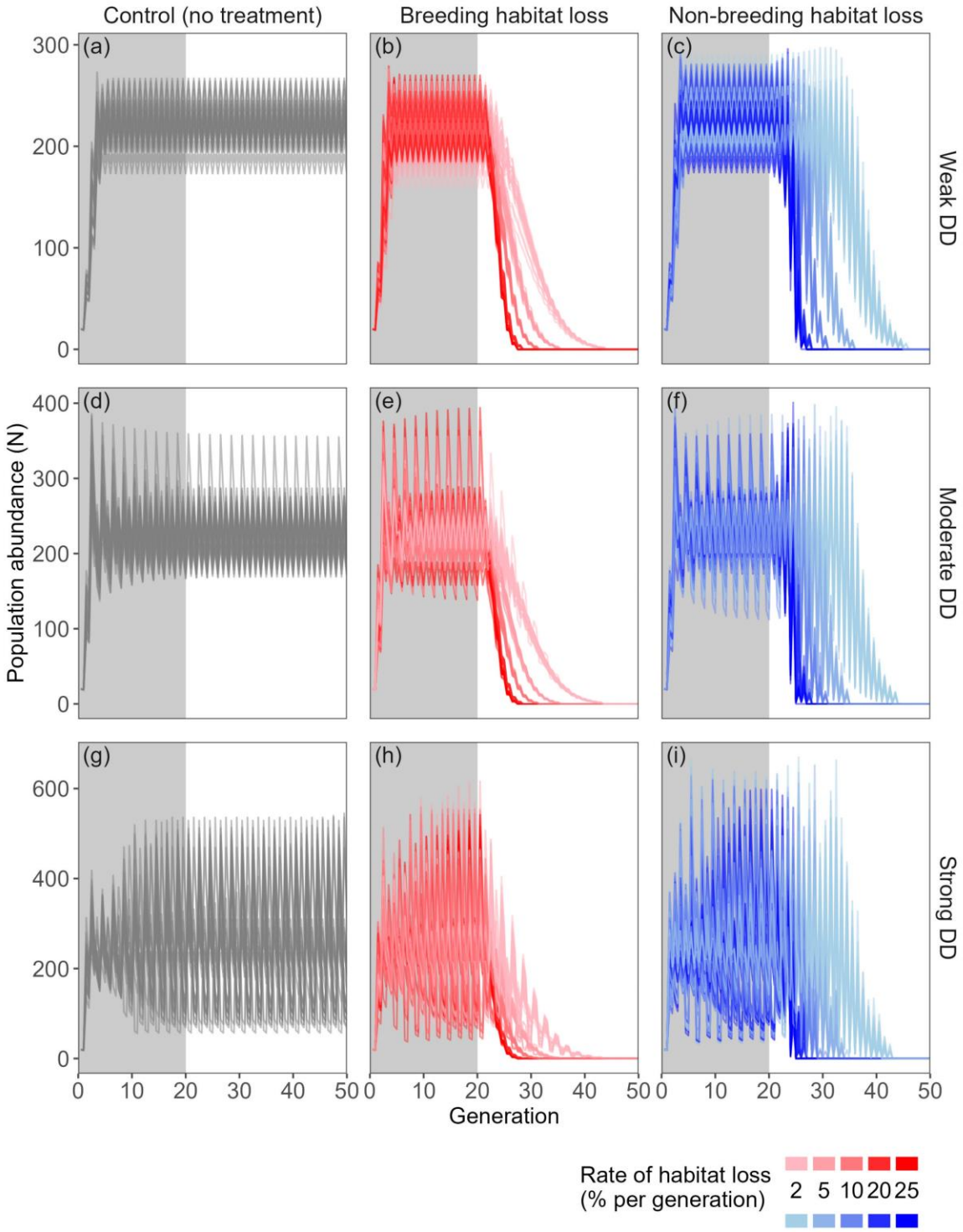
density dependence scenarios. (See *Model simulations* in *Methods*.) Sample size = 25 simulations per treatment.

Figure 4. Rate of habitat loss, strength of density dependence, and the timing of population collapse with season-specific habitat loss. To explore how the strength of density dependence influences the timing of population collapse, we parameterized our bi-seasonal Ricker model under three different theoretical scenarios of density dependence and using the experimental parameters obtained from our seasonal populations of *Drosophila* (see *Model simulations* in *Methods*). The time to extinction was calculated as the number of generations of season-specific habitat loss at a particular rate before the populations collapsed, excluding the 20 generations of 'pre-treatment' in which populations were simulated under control conditions.

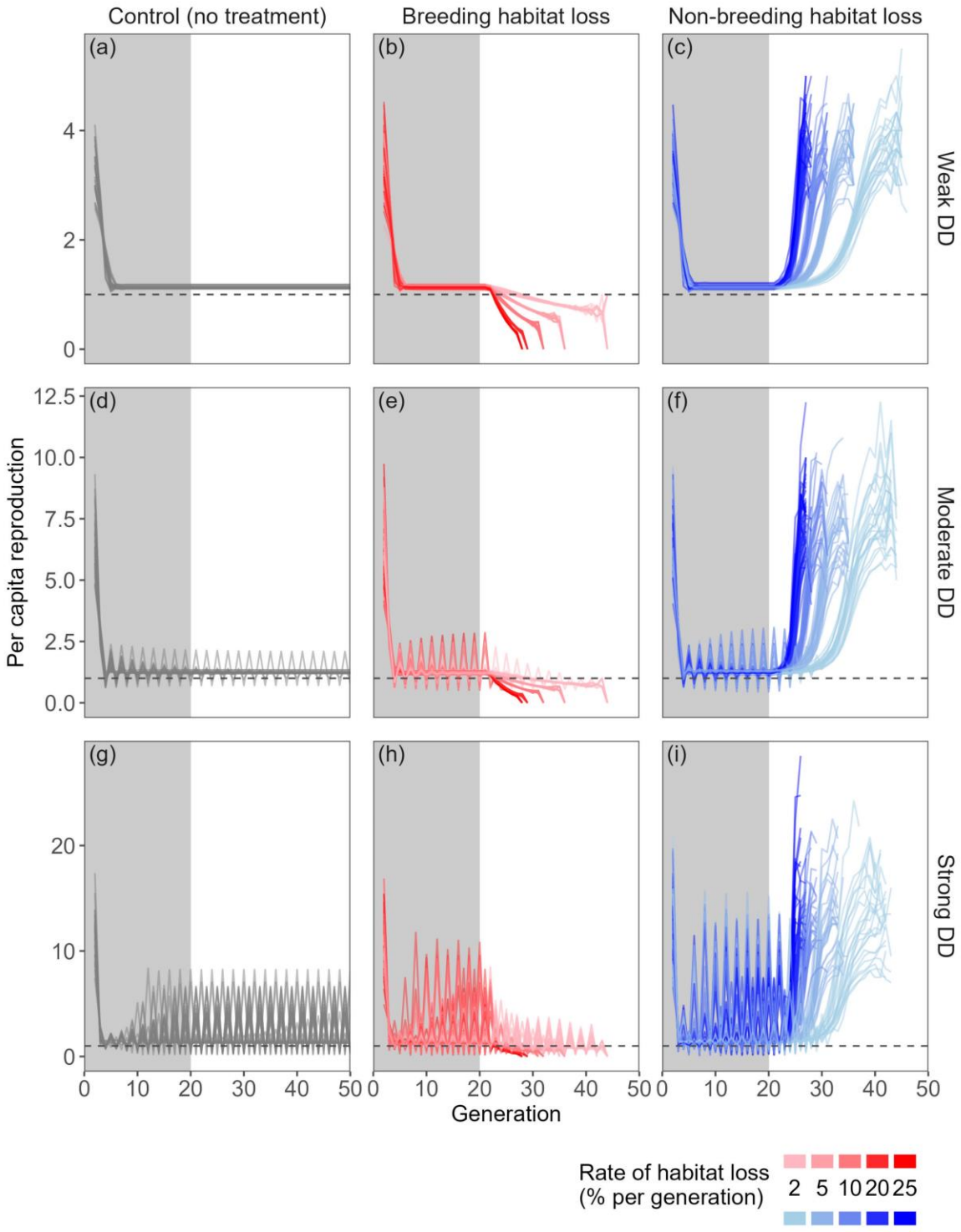
Figure 5. Effect of changing the strength of (a) non-breeding and (b) breeding density dependence for simulations of 10% non-breeding habitat loss. To explore the effect of density-dependence on time to extinction with non-breeding habitat loss, we systemically varied the strength of density dependence in either the breeding or non-breeding period, while holding density dependence constant in the other period (e.g., by setting breeding density dependence as moderate and vary the strength of non-breeding density dependence; see *Relative strength of density dependence* in *Methods*). Single, deterministic model runs were conducted for each pairwise combination of strengths of breeding and non-breeding density dependence. Extinction time was determined by performing a single iteration of the non-breeding habitat loss model with each combination of breeding and non-breeding strengths of density dependence.

Figures

Figure 1.



761 Figure 2.



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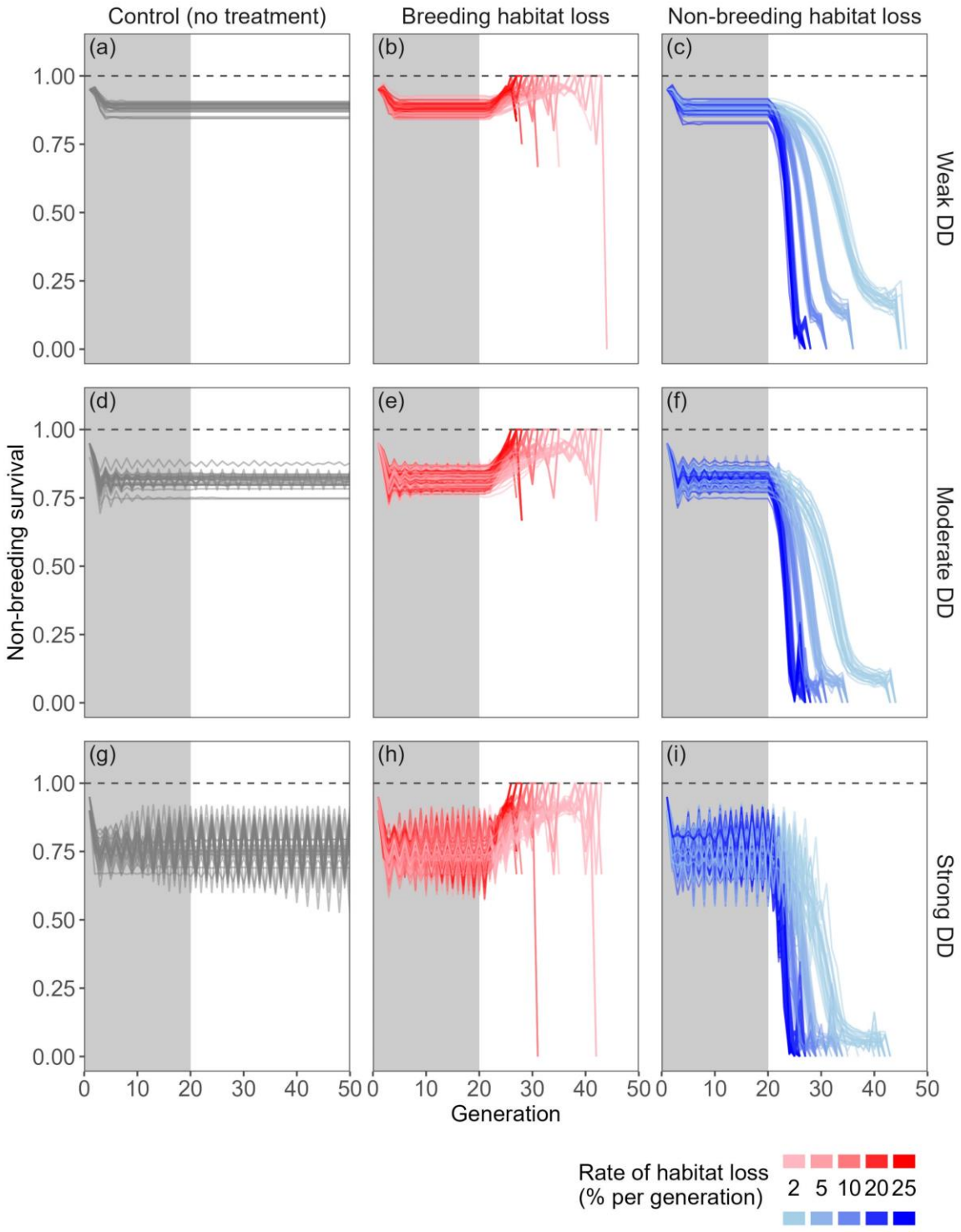
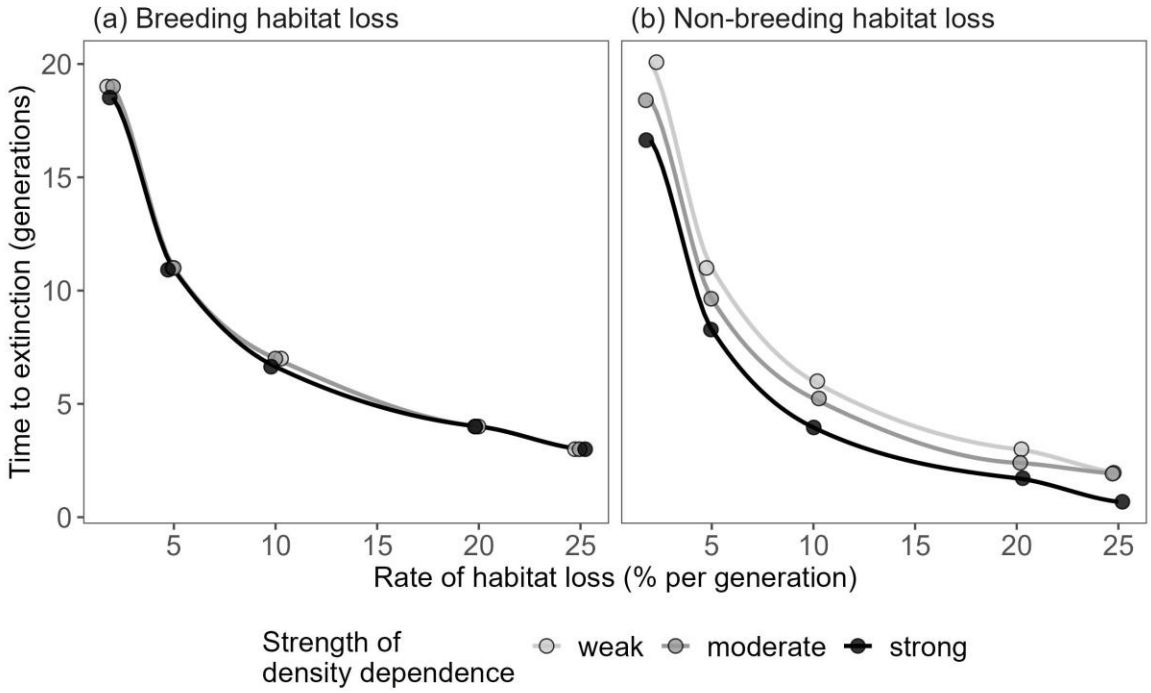
763 Figure 3.



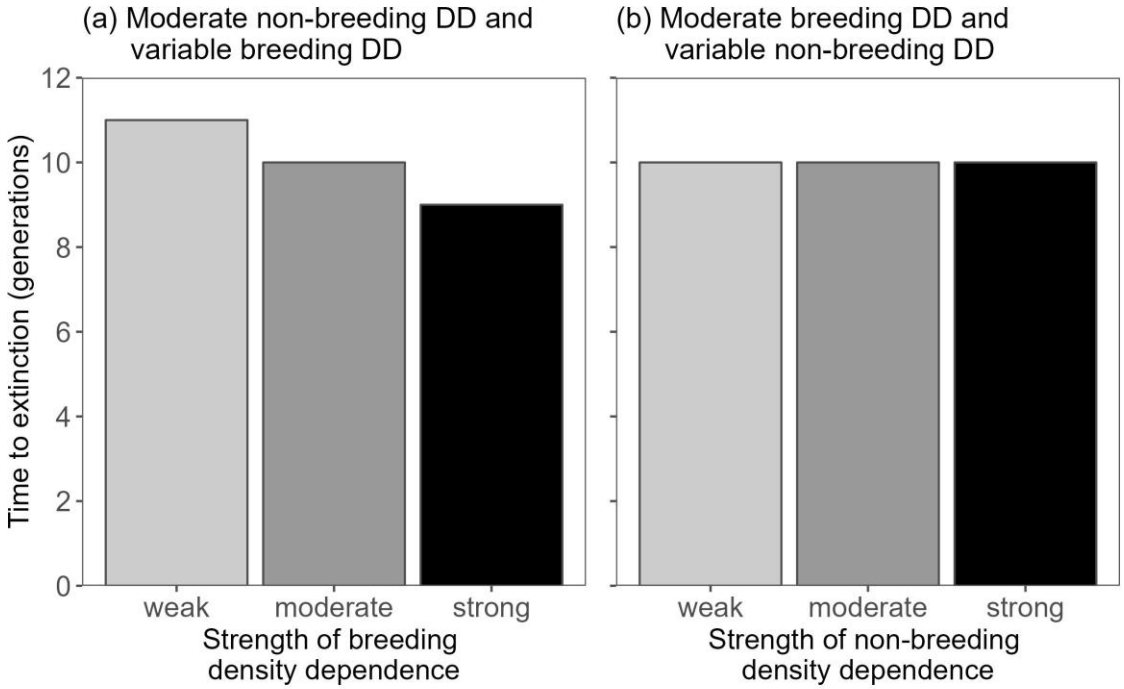
764

765 Figure 4.



766

767 Figure 5.



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