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RESEARCH ARTICLE

Eco-evolutionary dynamics of partially migratory metapopulations in spatially and seasonally varying environments

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Abstract

1. Interlinked population dynamic and evolutionary responses to spatial and seasonal environmental variation, stemming from interactions and feedbacks among phenotypic variation, genetic variation, selection and demography, could generate complex eco-evolutionary dynamics that span temporal and spatial scales.
2. Partially migratory metapopulations (PMMPs), featuring sequential seasonal sympatry and allopatry of different sets of resident and seasonally migrant individuals, have clear potential for such eco-evolutionary outcomes. This is because ongoing evolution of reversible seasonal migration affects spatio-seasonal population dynamics and densities, which could in turn shape forms and magnitudes of selection on migration, causing feedbacks on evolution. However, key environmental and genetic conditions that maintain migratory polymorphisms, and resulting eco-evolutionary dynamics of PMMPs given stochastic environmental variation and strong spatially restricted seasonal perturbations, have not been characterized.
3. We built a general individual-based model that tracks eco-evolutionary dynamics in PMMPs inhabiting spatially structured and seasonally varying landscapes, with seasonal migration formulated as a quantitative genetic threshold trait. Simulations showed that such genetic architectures and landscape structures, which are common in nature, readily produce stable partially migratory systems given diverse regimes of environmental variation.
4. Partial migration is maintained whenever sites differ in non-breeding season suitability, defined as variation in density-dependence, causing 'ideal free' non-breeding distributions where residents and migrants occur with frequencies generating similar survival probabilities. Further, bet-hedging can cause stable partial migration without any fixed differences in non-breeding season density-dependence among sites and even without density-dependence at all, given sufficiently large stochastic environmental fluctuations among sites and years.

5. Importantly, major local non-breeding season mortality events, as could result from extreme climatic events, generate eco-evolutionary dynamics that ripple out to affect breeding and non-breeding season space use of subpopulations throughout the PMMP, on both short and longer timeframes. These effects result from spatially divergent selection on the occurrence and destination of migration.
6. Our model thus shows how changing partial seasonal migration acts as a key mediator of eco-evolutionary dynamics in (meta)populations occupying spatially and seasonally varying environments. It thereby initiates new steps towards predicting responses of natural partially migratory populations to ongoing changes in spatio-seasonal patterns of environmental variation.

KEYWORDS
environmental stochasticity, extreme climatic events, liability, life-history trait, phenotypic polymorphism, seasonal migration, spatial ecology, threshold trait

1 | INTRODUCTION

Wild populations are currently experiencing rapid environmental changes, including increasing frequencies and severities of extreme climatic events (ECEs) such as droughts, heatwaves, floods and storms, which can be strongly seasonally and spatially variable (Hernández-Carrasco et al., 2025; Trenberth et al., 2015). Such variation can directly impact vital rates and thereby cause immediate population declines, and simultaneously cause episodes of strong natural selection on traits that mediate resilience or escape (Baeckens & Donihue, 2025; van de Pol et al., 2017). Resulting interlinked population and evolutionary dynamics could generate eco-evolutionary outcomes that reshape populations' geographical and phenotypic distributions (Ellner et al., 2011; Fouqueau & Polechová, 2024; Govaert et al., 2019). Integrated understanding of forms and mechanisms of eco-evolutionary dynamics induced by diverse regimes of seasonal environmental variation, including ECEs, is therefore required to predict overall population outcomes (Ferriere & Legendre, 2013; Kinnison & Hairston, 2007). Since such dynamics fundamentally require phenotypic and genetic variation in fitness-related traits, foundational questions of how such variation is maintained must also be addressed.

In the context of spatial and seasonal environmental variation, one influential form of phenotypic variation is partial seasonal migration, where breeding populations comprise mixtures of year-round resident individuals and seasonally migrant individuals that leave during the non-breeding season then return to breed (Chapman et al., 2011). Such partial migration is taxonomically and geographically widespread, occurring in many birds, reptiles, fish, amphibians and mammals, and involving short- or long-distance seasonal movements (Berg et al., 2019; Chambon et al., 2019; Dodson et al., 2013; Grayson et al., 2011). Such systems have substantial potential for complex eco-evolutionary dynamics and feedbacks involving spatial population dynamics occurring on seasonal timeframes (hereafter 'spatio-seasonal' dynamics). Specifically, spatial variation in seasonal environmental conditions can induce strong selection on phenotypic expression of seasonal migration versus residence, through direct effects on survival and/or carry-over effects on subsequent reproduction (Acker, Burthe, et al., 2021; Ohms et al., 2019; Reid et al., 2018). For example, non-breeding season ECEs that affect particular locations could impact either residents or particular sets of migrants, and hence cause strong selection for or against seasonal migration (Acker, Daunt, et al., 2021; Sanz-Aguilar et al., 2012). Resulting evolution of the degree and form of seasonal migration will reshape seasonal distributions of individuals from focal breeding populations and hence alter local seasonal densities (Kasai et al., 2018; Martin et al., 2022; Reid et al., 2018). Any density-dependence in vital rates could then cause frequency-dependence in fitness consequences of migration versus residence (Kaitala et al., 1993; Taylor & Norris, 2007), potentially feeding back to cause eco-evolutionary dynamics that could play out over spatial and temporal scales far exceeding the original ECE (Reid et al., 2018). However, such dynamics and their implications for the maintenance of migratory polymorphisms and overall population viability remain substantially unexplored.

Existing partial migration theory typically envisages simple two-site systems, comprising a breeding site that can be occupied all year and one other site that is only suitable in the non-breeding season (hence local breeding does not occur). Simple genetic architectures, such as a single locus with competing 'resident' and 'migrant' alleles, are commonly envisaged (Griswold et al., 2010; Kokko, 2011; Taylor & Norris, 2007), although both spatial and genetic model variations exist (Ohms et al., 2019; Reid et al., 2018; Taylor & Norris, 2010). Common conclusions are that stable partial migration requires balanced (i.e. equal) fitness of residents and seasonal migrants, and/or negative density-dependence in survival at the non-breeding and/or breeding sites generating negative frequency-dependent selection on seasonal migration (Griswold et al., 2011; Kaitala et al., 1993; Kokko & Lundberg, 2001; Lundberg, 1987; Ohms et al., 2019; Shaw & Levin, 2011; Taylor & Norris, 2007). Accordingly, partial migration is predicted to be maintained only under rather specific conditions. However, such predictions contrast with observations that partial migration is prevalent across highly diverse conditions in nature (Chapman et al., 2011), with unbalanced fitness consequences of alternative migratory strategies (Buchan et al., 2020). New models that examine the form and maintenance of partial migration, and that relax restrictive assumptions on spatial structures and forms of genetic variation, might insightfully reveal wider conditions that foster polymorphisms and resulting potential for spatio-seasonal eco-evolutionary dynamics.

First, the restrictive assumption that partial migration involves one population using two sites (i.e. breeding and non-breeding sites), and hence that migrants move into empty space, should be relaxed. In nature, seasonal migrants from any one population commonly arrive at sites holding year-round residents and/or seasonal migrants from other populations (Figure 1a). Such 'partially migratory metapopulations' (PMMPs; Reid et al., 2018), where different sets of resident and migrant individuals are allopatric versus sympatric in breeding and non-breeding seasons, occur widely (Austin et al., 2019; Berg et al., 2019; Geijer et al., 2016; Grayson et al., 2011; Lok et al., 2011; Papastamatiou et al., 2013; Sanz-Aguilar et al., 2012; Zúñiga et al., 2017), and imply very different properties from two-site models. Most notably, because non-breeding season density in a focal site is determined not only by the frequency of local outgoing seasonal migration from a focal population, but also by incoming seasonal migrants from other populations, any frequency-dependent selection on migration is likely to be weakened (Reid et al., 2018). Further, spatio-seasonal environmental variation could cause spatially divergent selection on migration that could foster stable system-wide partial migration (Reid et al., 2018). For example, if sites hold both local residents and incoming seasonal migrants during the non-breeding season, a major non-breeding season mortality event (due to an ECE or any other cause) would cause selection for seasonal migration in the local population (i.e. individuals that breed locally) but simultaneous selection for residence in populations from which incoming seasonal migrants originated. Additionally, stochastic spatio-seasonal environmental variation could potentially favour partial migration through genotype-level bet-hedging. Here, if parents can spread risk by producing offspring that use diverse non-breeding season locations (some residents, and some seasonal migrants to different destinations), variance in non-breeding season survival is reduced, facilitating lineage survival (Cohen, 1967; but see Lundberg, 1987).

Second, the assumption of a one-locus two-allele genetic architecture controlling seasonal migration versus residence should be relaxed. In many taxa, dichotomous migration versus residence is appropriately conceptualized as a quantitative genetic threshold trait (mammals: Berg et al., 2019; fish: Dodson et al., 2013; birds: Pulido, 2011). Here, individuals migrate or remain resident when an underlying continuously distributed 'liability' is above versus below a threshold (Acker et al., 2023; Dodson et al., 2013; Pulido, 2011). Liability depends on a heritable 'breeding value' shaped by alleles at many small-effect loci (i.e. the 'infinitesimal model'), alongside various environmental effects. Substantial latent ('cryptic') genetic variation can consequently exist among individuals expressing the same phenotype. Conditions that cause additional environmental effects on liabilities, and therefore cause new individuals to cross the threshold and express the alternative phenotype, can expose previously cryptic genetic variation to selection (Acker et al., 2023; Pulido, 2011). Such quantitative genetic threshold traits can therefore exhibit very different environmentally induced dynamics from simple Mendelian traits, or from traits that are continuously distributed on phenotypic scales (Reid & Acker, 2022). But, threshold trait architectures (as opposed to approximations that envisage evolving probabilities) have not been explicitly considered in eco-evolutionary theory, limiting prediction of joint phenotypic, evolutionary and population dynamics emerging in natural systems.

Accordingly, we designed a general individual-based model to quantify eco-evolutionary dynamics of PMMPs in spatially and seasonally varying landscapes, formulating expression of seasonal migration versus residence as a quantitative genetic threshold trait. First, we show that such systems can readily maintain partial migration, of forms and magnitudes that depend on spatial variation in non-breeding season environmental suitability. Second, we show that seasonal environmental stochasticity can generate partial seasonal migration, even without density-dependence in survival. Third, we demonstrate how major local perturbations, representing local seasonal ECEs, can induce eco-evolutionary dynamics that extend across substantial spatial and temporal scales. Our model and simulations therefore reveal key properties of spatially structured and potentially seasonally mobile populations, elucidating eco-evolutionary responses to increasingly variable seasonal environments.

2 | METHODS

We model a PMMP comprising defined subpopulations breeding in S separate sites, experiencing an annual cycle comprising sequential breeding and non-breeding seasons (e.g. summer and winter; Figure 1). Through each non-breeding season, individuals can stay resident at their breeding site or migrate to a different site before returning to their original site to breed the next year. Hence, non-breeding season destination sites for migrants from one subpopulation may also contain local residents in another subpopulation, generating combinations of 'shared breeding' and 'shared non-breeding' partial migration within the PMMP (Reid et al., 2018).

Population densities and seasonal environmental characteristics (termed 'suitability') at each site can affect vital rates during both seasons. Sets of sites can be constructed to caricature diverse landscapes and spatial scales. For example, envisaging a northern temperate latitudinal gradient with 'northern' sites providing good breeding season conditions and bad non-breeding season conditions and vice versa in the 'south,' or other common patterns such as altitudinal (Arnekleiv et al., 2022), coastal-to-inland (Allen et al., 2019), aridity (Serneels & Lambin, 2001) or salinity gradients (Kasai

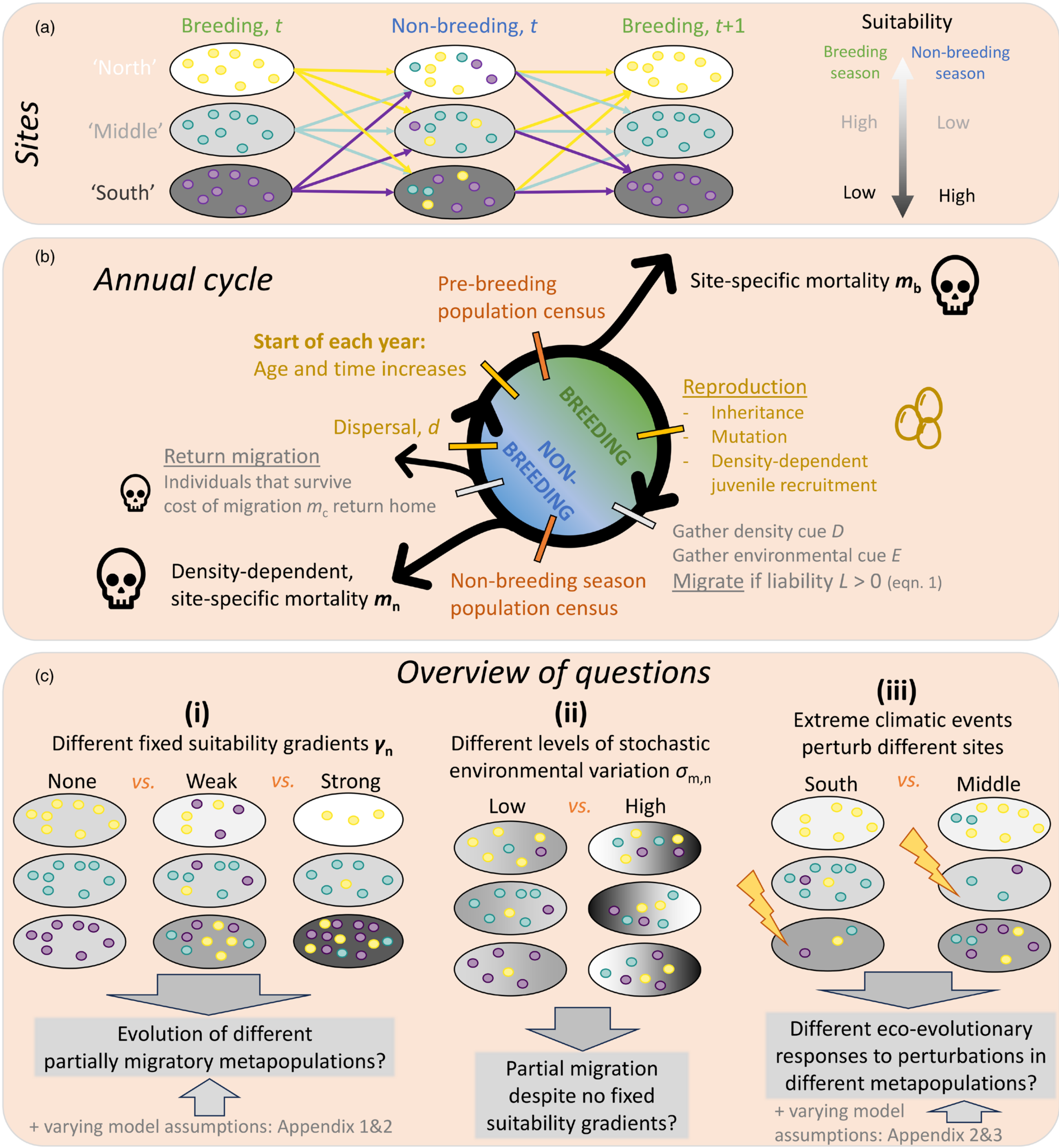

FIGURE 1 (a) Illustration of a partially migratory metapopulation (PMMP) with $S=3$ sites (greyscale ovals) and subpopulations defined by individuals breeding in each site (small circles, colour indicates breeding site). During the non-breeding season, individuals can stay in their breeding site or migrate to a different site (coloured arrows): Each site can then contain mixtures of residents and incoming seasonal migrants. For the following breeding season, all individuals return to their home site. Sites may differ according to breeding and/or non-breeding season suitability gradients. (b) Order of events in the modelled annual cycle. Each year starts with the breeding season (green), followed by the non-breeding season (blue). Black: Mortality events (with skulls). Grey: Seasonal migration. Orange: Population census. Gold: Individual genes and properties change. Parameters in bold indicate vectors of site-specific values. (c) Overview of questions addressed. In (a) and (c), lighter versus darker grey ovals represent sites that are less versus more suitable during the non-breeding season (for simplicity labelled 'north' versus 'south', but could be any spatial gradient).

et al., 2018), or ponds along a gradient of ephemeral to permanent (Grayson et al., 2011). Such environmental gradients can exist in either, neither or both seasons. Landscapes are spatially implicit, such that the geographical arrangement of sites is not limited to linear or other specific constellations, but can be parameterized to capture any desired landscapes.

2.1 | Migration trait architecture

Expression of seasonal migration versus residence is modelled as a quantitative genetic threshold trait, where individual i migrates in year t if its liability $L_i(t)$ exceeds a threshold value T (Figure 1b; e.g. Acker et al., 2023; Pulido, 2011; Roff, 1996). $L_i(t)$ comprises three components: a heritable additive genetic effect (i.e. its 'breeding value') a_i; a deterministic environmental effect defined by local population density, D; and a stochastic environmental effect, E (Equation 1). The value of D at site j at time t is the ratio of the subpopulation size $n_j(t)$ to the site's carrying capacity K_j, $D_j(t) = n_j(t) / K_j$. The value of E is given by a random draw from a normal distribution of mean 0 and variance 1, acting at either the site level ('coarse-grained' environments, where all individuals in site j experience the same $E_i = E_j$), or at the individual level ('fine-grained' environments, where each individual experiences a different E_i). This stochastic environmental effect on liability represents the net effect of any hypothetical combination of breeding season factors (e.g. weather, food availability, body condition) beyond the considered deterministic effect of density, as is a standard general conceptual formulation in quantitative genetics.

Liability-scale reaction norms are assumed to be linear, so for individual i in site j in year t,

$$L_i(t) = a_i + \beta_D D_j(t) + \beta_E E_i(t). \quad (1)$$

Here, the coefficients β_D and β_E can be independently adjusted to alter the impacts of the non-genetic effects (D and E, respectively) on $L_i(t)$ relative to each other and to the additive genetic effect a_i. While D is always positive (and near 1 for subpopulation sizes near K), E is white noise (equally often negative or positive). Hence, when β_E is non-zero, expected $L_i(t)$ translates probabilistically into expression of migration versus residence (Reid & Acker, 2022). Consequently, individuals can switch phenotypes between years (effectively representing 'facultative' migration). Here, both 'facultative' and effectively 'obligate' (i.e. phenotypically invariant) residence or migration can emerge from the same underlying genetic architecture depending on the proximity of the expected $L_i(t)$ to T (which affects the degree to which draws of $\beta_E E_i$ cause individuals to cross the threshold). For current purposes of illustrating broad conceptual points, we set β_D and β_E as fixed non-evolving parameters. Modelling evolution of β_D and β_E, and hence of liability-scale plasticity, is outside our current scope. Accordingly, we do not imply evolutionary optimization of the environmental components of $L_i(t)$.

We assume that the 'breeding value', a_i, is controlled by many loci of small effect so that inheritance and mutation is governed by the infinitesimal model (Barton et al., 2017). Here, an offspring's a_i is drawn from a normal distribution with mean equalling the mean of its parents' breeding values, and variance equal to the initial subpopulation additive genetic variance, V_0 (ignoring inbreeding, which is negligible given large populations).

To dispatch seasonal migrants to their non-breeding season locations (conditional on migrating), we let an unlinked haploid gene determine an individual's non-breeding season destination. For simplicity, we envisage one allele that directs towards each site, where an individual's allele can direct towards any site other than its breeding site. Such large effect loci determining migratory destinations exist in nature (e.g. Sokolovskis et al., 2023), and this formulation allows ideal free non-breeding season distributions to evolve (see below). Since the destination gene is not expressed unless an individual migrates, selection on this locus is weaker the less seasonally migratory the population (Van Dyken & Wade, 2010). We assume Mendelian segregation where each offspring inherits the destination allele of one random parent, essentially representing a diploid system with no dominance (i.e. no allele on average overrules the other). This allele mutates to one of the S–2 other possible alleles with probability μ. Higher μ generates imperfect transmission, which is also broadly interpretable as environmental noise (Appendix S1).

2.2 | Annual cycle

Populations are sexually reproducing and age-structured with overlapping generations. Each year (Figure 1a), all individuals age at the start of the breeding season. Density-independent breeding season mortality $m_{b,j}$ then occurs (potentially varying among sites, j), followed by density-dependent reproduction. Here, individual reproductive success depends on a 'maximum fecundity' f (expected number of recruited offspring per parent at low population densities), and the number of 'slots' available at breeding site j, $K_j - n_j$. Specifically, n_{off} offspring recruit, where $n_{off} = \min(K_j - n_j,\ n_j f)$, such that post-breeding subpopulation sizes (juveniles + adults) cannot exceed K_j. We assume random polygynandrous mating, sampling (with replacement) n_{off} mothers and n_{off} fathers among all surviving adults. Consequently, selfing is not prohibited, although the probability is tiny given large populations.

At the start of the non-breeding season, individuals migrate if $L_i(t) > T$ (Equation 1, where $T = 0$ by convention). Then, local density-dependent non-breeding season mortality $m_{n,j}$ occurs, as is postulated to be a key process shaping partial migration (Kaitala et al., 1993; Taylor & Norris, 2007). $m_{n,j}$ is an exponential function of the number of individuals $n_j(t)$ present in each site j,

$$m_{n,j} = \left(1 - \exp\left\{-\frac{\gamma_{n,j} n_j(t)}{K_j}\right\}\right) + \varepsilon_j \quad (2)$$

where ε_j is a stochastic term sampled from a normal distribution with mean 0 and variance $\sigma_{m,n}^2$. $m_{n,j}$ is bounded between 0 and 1, with higher or lower values resulting from draws of ε_j absorbed at the boundaries. The strength of density-dependence is deterministically modulated by the site-specific parameter $\gamma_{n,j}$, representing local seasonal 'suitability'. This mortality occurs independently of whether individuals that are currently present are resident at site *j* or temporarily migrated there from elsewhere. We set *K* constant across sites and seasons, and implement varying site quality through varying $\boldsymbol{m}_b$ and $\boldsymbol{\gamma}_n$ (bold denotes a vector of site-specific values).

Finally, all individuals that migrated return to their breeding site, but die with a probability m_c, representing a mortality cost of migration. Before the next breeding season, dispersal (i.e. movement between different breeding sites) occurs with a fixed probability *d*, where dispersers move to a random new subpopulation. Dispersal is unrelated to an individual's migratory status. Thus, individuals are not precluded from dispersing back to the site they just migrated from, effectively representing failure to return from migration. If dispersal occurs, a random destination allele for subsequent seasonal migration is drawn, directing to any other site apart from the individual's new breeding site. Offspring of dispersed individuals start breeding in their natal site and can inherit their parent's (new) destination allele. For current purposes we primarily consider a fixed small dispersal probability ($d=0.01$), thereby generating some gene flow among breeding subpopulations, potentially constraining local adaptation in liability and destination of seasonal migration. This captures observed low dispersal rates observed in many natural PMMPs, where breeding populations are substantively geographically distinct despite non-breeding season admixture (Barlow et al., 2013; Poole et al., 2024; van de Pol et al., 2014). Throughout, *d* is constant rather than evolving: investigating coevolutionary dynamics of dispersal and seasonal migration exceeds our current scope (see Section 4).

To quantify spatio-seasonal population dynamics and underlying degrees and forms of seasonal migration, we censused all individuals present at each site at two annual time points: breeding season before reproduction, and non-breeding season before mortality and return migration (Figure 1b). To quantify evolutionary dynamics underlying observed population dynamics, we recorded individual-level characteristics (breeding site, age, liability $L_i(t)$, breeding value a_i and migration destination allele) before breeding in each subpopulation at set intervals through each simulation.

2.3 | Simulations

Our model framework can be parameterized to envisage diverse spatial structures, landscapes, life-histories and genetic and environmental effects underpinning migration. Numerical analysis of the full potential parameter space is consequently impossible. Accordingly, we undertook targeted eco-evolutionary simulations designed to examine and illustrate three key conceptual points.

First, we quantified effects of different spatial gradients of seasonal suitability on the evolution and maintenance of PMMPs (Figure 1ci). We independently set whether breeding season mortalities $\boldsymbol{m}_b$ and/or non-breeding season suitabilities $\boldsymbol{\gamma}_n$ exhibited weak or strong spatial gradients, or else were equal across sites. Here, for simplicity, we term our sites 'north', 'middle' and 'south', mimicking a northern hemisphere latitudinal gradient. However, the model and simulations make no explicit assumption on the sites' spatial arrangements and could equally be interpreted as other gradients (e.g. altitudinal).

Second, we tested the ability of environmental stochasticity to generate partial migration in the absence of any set spatial gradient in seasonal suitabilities (all $\boldsymbol{\gamma}_n=1/3$), by including random spatio-temporal variation in non-breeding season mortalities ($\sigma_{m,n}>0$, Figure 1cii). Seasonal mortality is thus unpredictable and uncorrelated among sites and years. We also tested whether such environmental stochasticity could maintain partial migration even without any non-breeding season density-dependence ($\boldsymbol{\gamma}_n=0$), a process often postulated to be central to the evolution of stable partial migration.

Third, to quantify eco-evolutionary responses of PMMPs to specific extreme climatic events (ECEs), we imposed a large non-breeding season perturbation on a single site (Figure 1ciii). This one-off event kills 80% of all individuals present, independent of whether they were residents or migrants from elsewhere, as occasionally observed in natural PMMPs (e.g. Alonso-Andicoberry et al., 2002; Frederiksen et al., 2008). We perturb each site separately in PMMPs that had previously evolved with strong, weak or no suitability gradients ($\boldsymbol{\gamma}_n$) and no stochasticity in non-breeding season survival ($\sigma_{m,n}=0$). These perturbations were designed to clearly reveal general eco-evolutionary responses and their underlying mechanisms: weaker ECEs (<80% mortality) induce the same demographic and evolutionary mechanisms, but with weaker effects.

Given our current objective of highlighting general conceptual points, we did not parameterize our simulations to capture details of any particular real system, but envisaged a broadly bird-like life history. All parameter values and definitions are summarized in Table S1. In brief, we primarily set $f=3$ and $\boldsymbol{m}_b=0.1$, with $\beta_D=0.1$, $\beta_E=1$, $\mu=0.01$ and $m_c=0.02$. We ran further simulations to quantify effects of varying key assumptions and parameter values (lower *f*, β_D and β_E set to 0, higher μ, higher or zero dispersal *d*, coarse- versus fine-grained environmental variation, and distance-dependent versus distance-independent cost of migration, Appendices S1–S3). Simulations were initiated with all subpopulations at $K=1000$, Poisson age distributions with mean 3 (near the average lifespans captured in most of our scenarios), and Gaussian breeding value distributions with mean 0 (equalling the migration threshold) and variance $V_0=1$. Each individual's destination allele was randomly assigned, excluding the allele encoding their home site. We primarily consider landscapes with $S=3$ sites, generating the simplest possible PMMP where individuals can either stay resident through the non-breeding season or migrate to >1 alternative sites. However, we additionally explore systems with $S=5$ sites (Appendix S2), allowing a wider range of migratory patterns, including 'leapfrog' and 'chain' migration (Lundberg & Alerstam, 1986).

Simulations were typically run for 10,000 years with 20 replicates per parameter set, ensuring that eco-evolutionary trajectories stabilize and adequately capturing among-replicate variation in outcomes. Simulations with stochastic mortality were run for 50,000 years, since evolutionary responses to such stochasticity are slower and more subtle (Simons, 2002). Individual attributes were recorded every 50 years. All simulations were run in R version 4.2.1 (R Core Team, 2022). Code is available at https://doi.org/10.5061/dryad.1rn8pk12n (Haaland et al., 2026). No ethical approval was required for the study.

3 | RESULTS

3.1 | Gradients of seasonal suitability

Our first results demonstrate the general point that partial seasonal migration can readily evolve and be maintained given a multi-site PMMP structure with sufficiently large differences among sites in non-breeding season suitability (i.e. strengths of density-dependence γ_n) coupled with a quantitative genetic threshold trait architecture (Figure 2a–c). Here, fully (i.e. entirely) migratory, partially migratory and fully resident subpopulations can all emerge from the same underlying architecture, respectively characterized by liability distributions that become entirely positive, span zero, or become entirely negative, achieved through evolutionary change in mean breeding value (Figure 2d–f).

Accordingly, with no suitability gradient, fully resident populations evolve (Figure 2a,d). Otherwise, subpopulations breeding in sites that are more, or less, suitable in the non-breeding season (heuristically termed 'south' and 'north') became less or more migratory respectively (Figure 2b,c,e,f). Further, depending on the costs of migration m_c and the steepness of the non-breeding

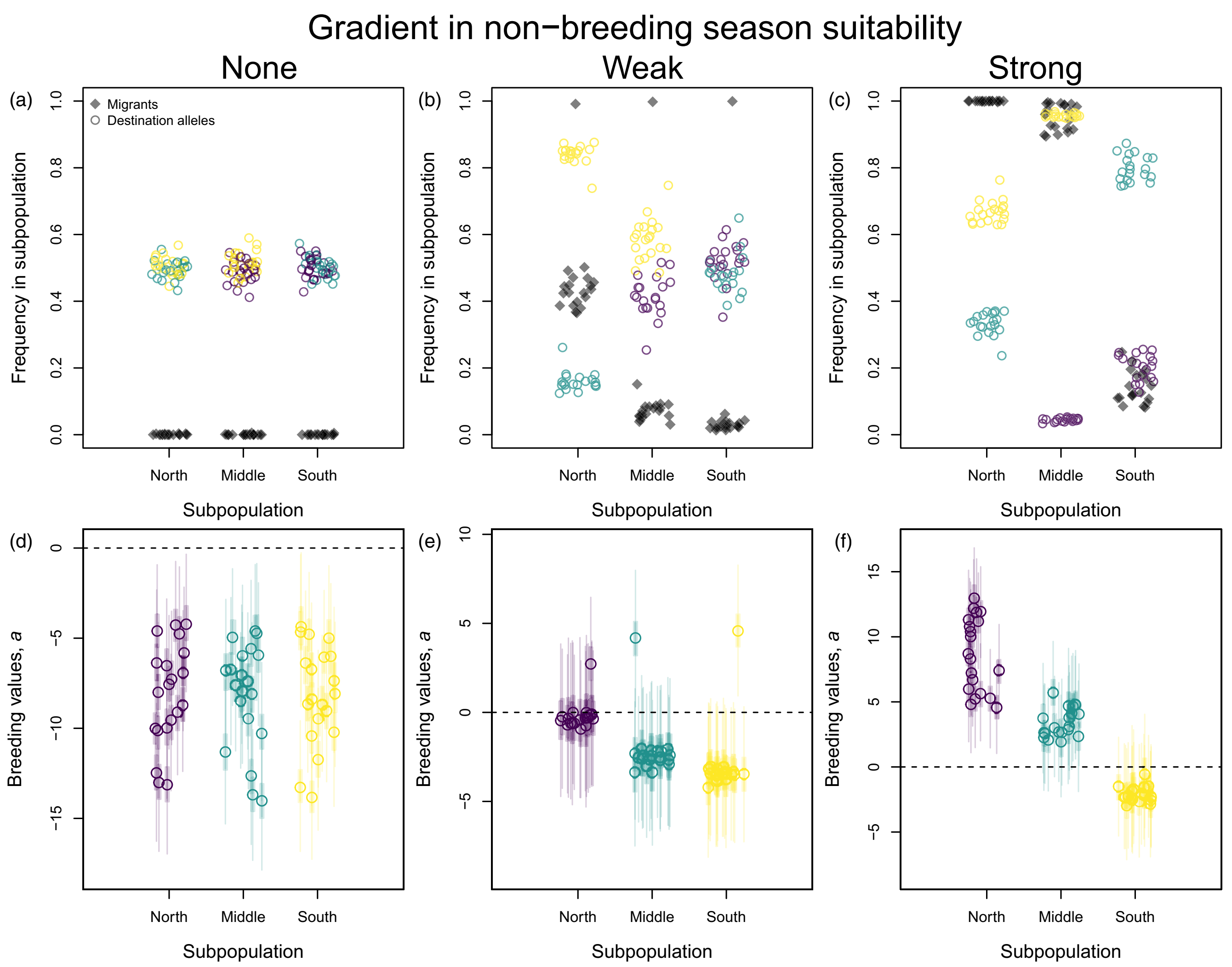

FIGURE 2 Metapopulation genetic structure after 10,000 years of evolution where sites experience (a, d) no, γ_n = {1/3,1/3,1/3}, (b, e) weak, γ_n = {1/2,1/3,1/5}, or (c, f) strong, γ_n = {5,1/2,1/10}, differences in non-breeding season suitability. (a–c) Migrant frequency (black diamonds) and destination allele frequencies (coloured circles; purple, green and yellow respectively represent alleles for the north, middle and south site) in each subpopulation, averaged across 50-year intervals through the last 1000 years within each simulation. Partial migration has evolved when black diamonds are away from 0 or 1. (d–f) Median (dark coloured circles), interquartile range (light coloured bars) and full range (thin coloured lines) of breeding values for migration liability in each subpopulation in year 10,000 for each simulation. Dashed horizontal lines show the threshold T = 0, above which individuals migrate. Note that y-axis scales differ. All parameters except γ_n have baseline values (Table S1).

season suitability gradient (γ_n), subpopulations can be partially migratory in the north and fully resident in the south (weak gradients, Figure 2b,e), or fully migratory in the north and partially migratory in the south (strong gradients, Figure 2c,f). This seemingly maladaptive migration in the south, and occasional fully migratory metapopulations (outliers in Figure 2b,e), is caused by gene flow due to dispersal among subpopulations constraining local adaptation (confirmed by additional simulations with higher or zero dispersal probabilities; Figures S4 and S5).

With weak non-breeding season suitability gradients, PMMPs evolved migration rates and destinations such that non-breeding season distributions of individuals generated similar density-dependent seasonal survival probabilities across sites (Figure 3b). Survival was slightly higher in the south site at equilibrium, but this site receives most seasonal migrants who also pay a cost of migration m_c, thereby evening out year-round survival probabilities. Hence, these simulations show how approximately balanced average fitness effects of residence and migration can emerge as an endpoint of the evolution of liability to migrate and resulting partial migration, rather than being specified upfront with fixed parameter values (as typically done elsewhere; Cobben & van Noordwijk, 2016; Fryxell & Holt, 2013). However, non-breeding season survival probabilities differed more among sites given strong suitability gradients (Figure 3c), implying that evolution of liability to migrate cannot fully compensate for the specified spatio-seasonal pattern of density-dependence. In contrast, differences among sites in breeding season

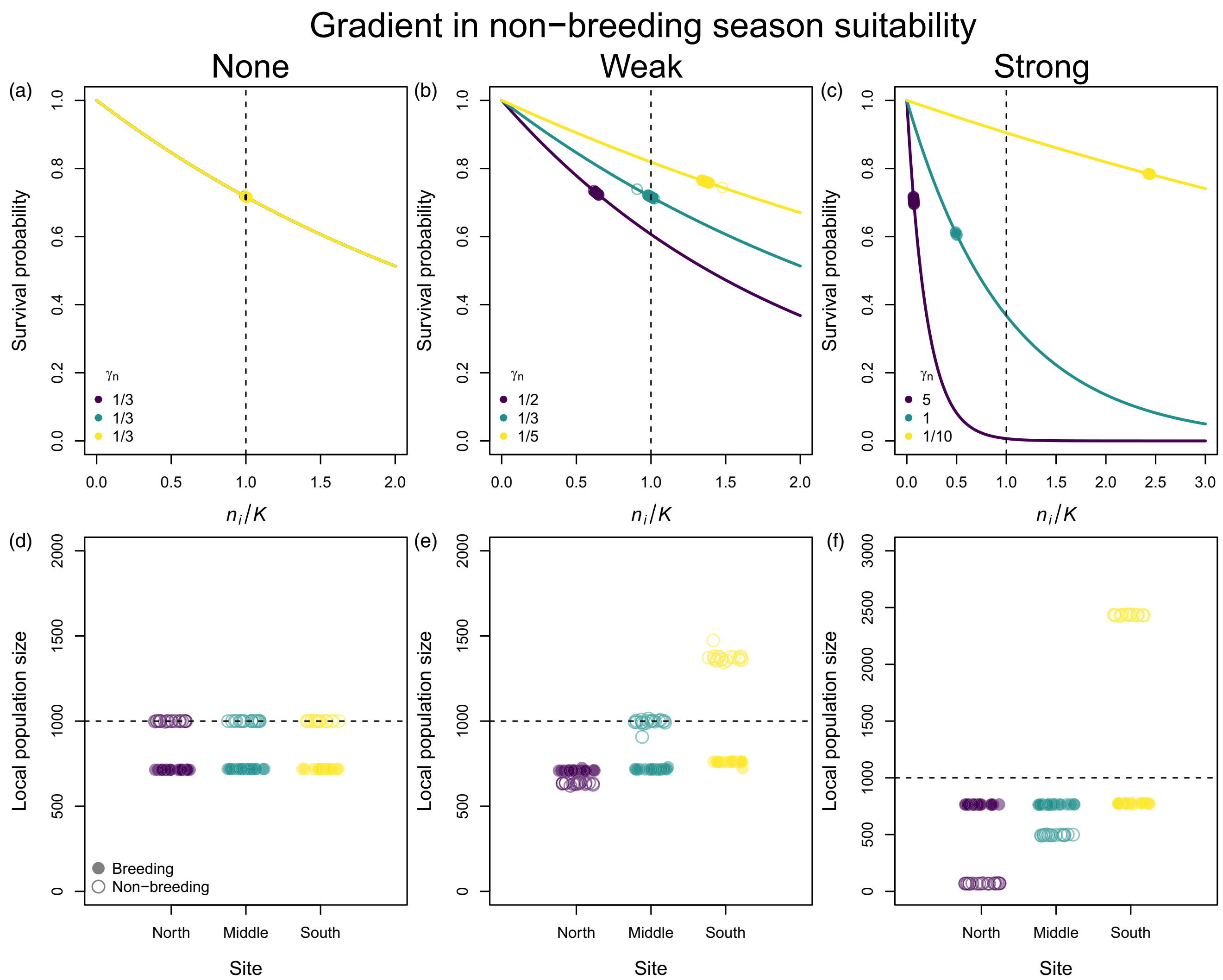

FIGURE 3 Metapopulation space use after 10,000 years of evolution where sites experience (a, d) no, γ_n = {1/3,1/3,1/3}, (b, e) weak, γ_n = {1/2,1/3,1/5}, or (c, f) strong, γ_n = {5,1/2,1/10}, differences in non-breeding season suitability. (a–c) Density-dependent non-breeding season survival (purple, green and yellow, respectively, represent north, middle and south sites), that is $1-m_{n,j}$ (Equation 2). Open circles along the lines show actual non-breeding season space use and survival probabilities averaged across the last 1000 years of each simulation; filled circles are means across replicate simulations. With no non-breeding season suitability gradient (a), all lines and circles overlap, with yellow plotted last. (d–f) Local population sizes during breeding (filled circles) and non-breeding seasons (open circles) at each site, averaged across the last 1000 years within each simulation. Dashed lines show carrying capacity. Note that y-axis scales differ. All parameters except γ_n have baseline values (Table S1).

mortality (m_b) did not affect migration liability or destination. Indeed, simulations with suitability gradients only affecting breeding season mortality generate fully resident metapopulations, mirroring the case with no suitability gradients (Figures 2a,d and 3a,d). Further, simulations with suitability gradients in both seasons generated very similar PMMPs to those evolving with non-breeding season suitability gradients only (results not shown).

The result that partial migration readily arises when sites differ in non-breeding season suitability remained robust when other model components were varied (Appendix S1). This includes whether the non-genetic components *D* and *E* (respectively local population density and stochastic environmental effects) contributed to migration liability or not, and whether environmental stochasticity was coarse- or fine-grained, because breeding values always evolved to compensate for the suite of other effects. However, coarse-grained variation increased among-year variation in numbers of migrants versus residents. Consequently, balanced fitness effects across residents and migrants were only evident on average across multiple years, not necessarily over shorter timeframes (Figure S2).

Qualitatively similar patterns also emerged given larger PMMPs ($S=5$ sites) and when the mortality cost of migration increased with distance travelled (Appendix S2). While distance-dependent costs did not limit the conditions where partial migration evolved, they shifted the resulting pattern of migration from 'leapfrog' to 'chain'. Specifically, rather than migrants from northern subpopulations travelling all the way south, some northern migrants travel to middle sites, and higher non-breeding season population densities in those sites in turn cause an increased proportion of individuals from middle sites to travel south.

3.2 | Stochasticity in survival

Simulations with intermediate levels of stochasticity in non-breeding season survival caused partial migration even without any fixed suitability gradient across sites (i.e. equal density-dependence, Figure 4a). Meanwhile, low stochasticity generated full residence, while very high stochasticity frequently drove metapopulations extinct (Figure 4a). Here, extinct metapopulations exhibited similar pre-extinction migratory frequencies as surviving replicates.

Further, beyond generating partial migration in the absence of among-site variation in non-breeding season suitability, environmental stochasticity even generates partial migration in the absence of any density-dependence at all (Figure 4b). Indeed, partial migration caused by environmental stochasticity persisted under broader parameter space with density-independent than density-dependent survival, because extinction rates were lower. This is notable given that non-breeding season density-dependence has previously been considered necessary for the evolution and maintenance of partial migration (Kaitala et al., 1993; Ohms et al., 2019; Taylor & Norris, 2007).

3.3 | Effects of extreme climatic events (ECEs)

Eco-evolutionary responses of PMMPs to specific non-breeding season ECEs depended on both the location of the perturbed site within the PMMP and the previously evolved migratory dynamics (Figure 5). Before the ECE (vertical dotted lines in Figure 5), all subpopulations were stable below *K* (pre-breeding censuses are plotted

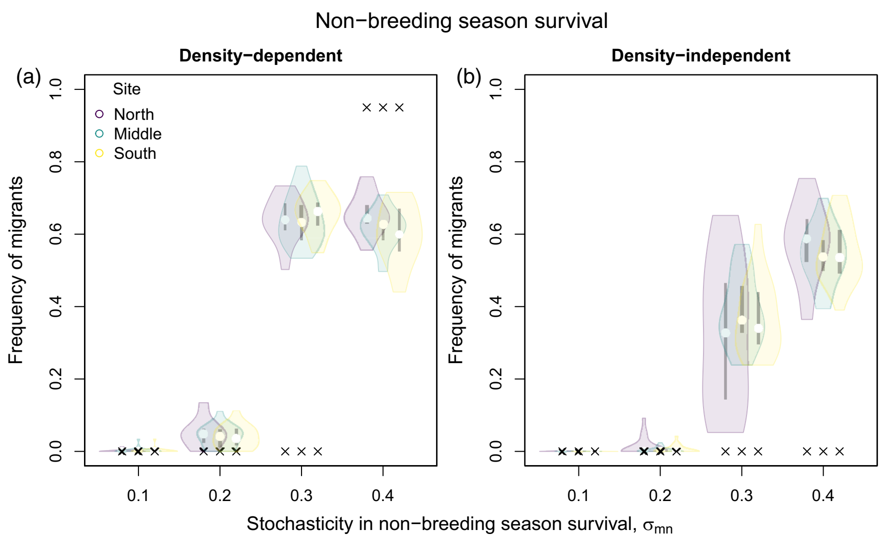

FIGURE 4 Evolved metapopulations with no fixed differences among sites in non-breeding season suitability, but stochastic variation in survival $\sigma_{m,n}$ among sites and years. Non-breeding season survival is (a) density-dependent, $\gamma_n=\{1/3,1/3,1/3\}$, or (b) density-independent, $\gamma_n=\{0,0,0\}$. Shaded areas denote densities of the frequency of migrants after 50,000 years of evolution for 20 replicate simulations, averaged across 50 year intervals through the last 1000 years. Purple, green and yellow, respectively, represent north, middle and south subpopulations. Open circles show medians, black boxes show interquartile ranges and black crosses show proportions of simulations ending with subpopulation extinction. Frequencies of migrants for extinct subpopulations (for $\sigma_{m,n}=0.4$ in (a)) are calculated across 50 year intervals through the last 1000 years before subpopulation extinction.

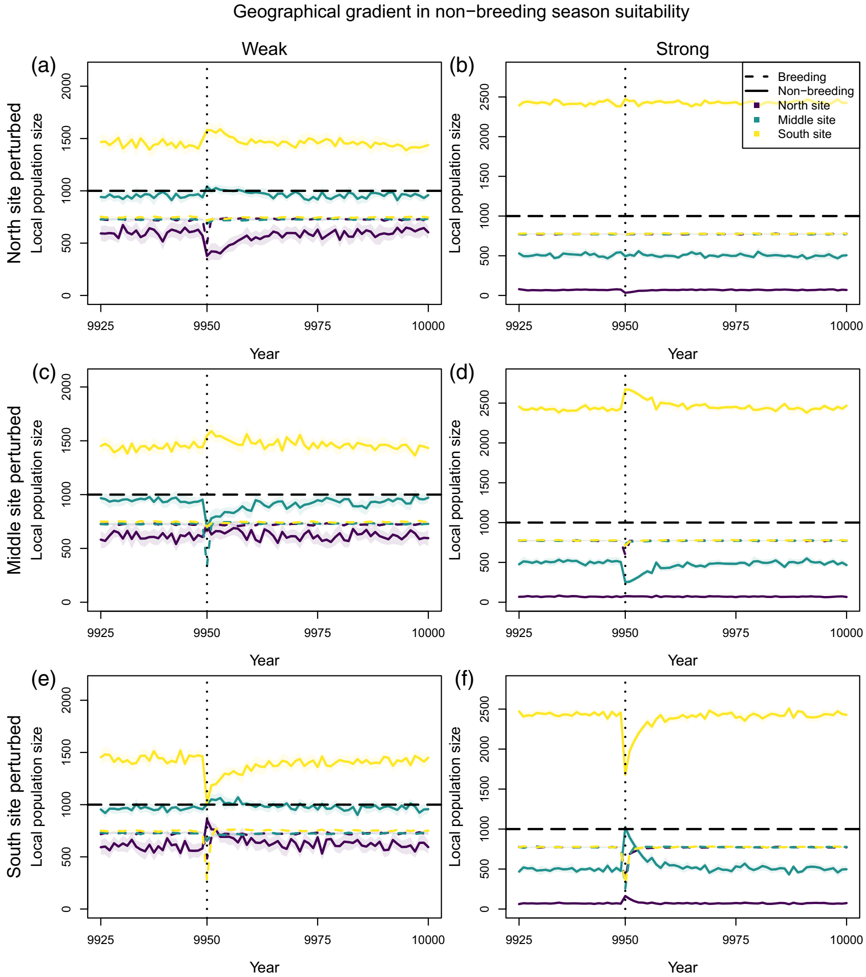

FIGURE 5 Dynamics of evolved partially migratory metapopulations before and after a non-breeding season extreme climatic event (ECE) in year 9950 (vertical dotted lines), striking the (a, b) north, (c, d) middle, or (e, f) south site, given (a, c, e) weak ($\gamma_n=\{1/2,1/3,1/5\}$) or (b, d, f) strong ($\gamma_n=\{5,1/2,1/10\}$) non-breeding season suitability gradients. Breeding (dashed coloured lines) and non-breeding season (solid coloured lines) local population sizes are shown for each site (purple, green and yellow representing north, middle and south sites respectively). Thick coloured lines and opaque bands represent means and 95% CI across 20 simulations. Dashed black lines show carrying capacity. Other parameters have baseline values (Table S1).

so mortality through the annual cycle reduces population sizes). As is intuitive, non-breeding season ECEs impact the local subpopulation, and the whole PMMP, more strongly when more individuals are present at the impacted site (Figure 5; Appendices S2 and S3).

For example, given strong non-breeding season suitability gradients, the north subpopulation is fully migratory, and the north site receives few incoming migrants from other subpopulations. Consequently, a local non-breeding season ECE has little effect on any subpopulation (Figure 5b). In contrast, an ECE at the middle or south site affects not only the local subpopulation by impacting local residents, but also the northern subpopulation(s) by impacting incoming migrants originating from there. The local subpopulation experiences an immediate decrease in both non-breeding and breeding season population sizes (Figure 5c–f). The breeding population quickly recovers demographically, due to increased recruitment of juveniles as density-dependence in breeding success is effectively relaxed. However, non-breeding season space use involves both residents and migrants, and needs to recover evolutionarily, which takes longer (about 20 years in the illustrated case, Figure 5c–f). This is because the ECE causes three simultaneous evolutionary effects (illustrated in Figure 6 for an ECE at the southern site).

First, it causes strong selection against residence in the subpopulation breeding at the impacted site, increasing mean breeding values for liability to migrate (Figure 6a, yellow line). Second, it causes selection against migration in all other subpopulations, decreasing mean breeding values (Figure 6a, purple and green lines). This response to selection is greater in subpopulations from which more individuals migrated to the impacted site. Third, it causes selection against migrating to the impacted site, thereby altering frequencies of the destination alleles in all other subpopulations (Figure 6b,c). The latter two effects are manifested as a sharp increase then gradual decrease in non-breeding season density in other sites following the ECE impact (Figure 5d,f), due to higher proportions of local residents plus influxes of migrants from other subpopulations.

Together, these effects cause a medium-term decrease in non-breeding season density in the perturbed site, which is balanced by concurrent increases elsewhere. Thus, while breeding season subpopulation sizes recover relatively fast (~5 years), and can even temporarily overshoot pre-ECE densities (due to weaker non-breeding season density-dependent mortality when fewer migrants arrive in the years following the ECE), non-breeding season space use takes much longer to return to pre-ECE equilibria (~15–25 years, Figure 5c–f).

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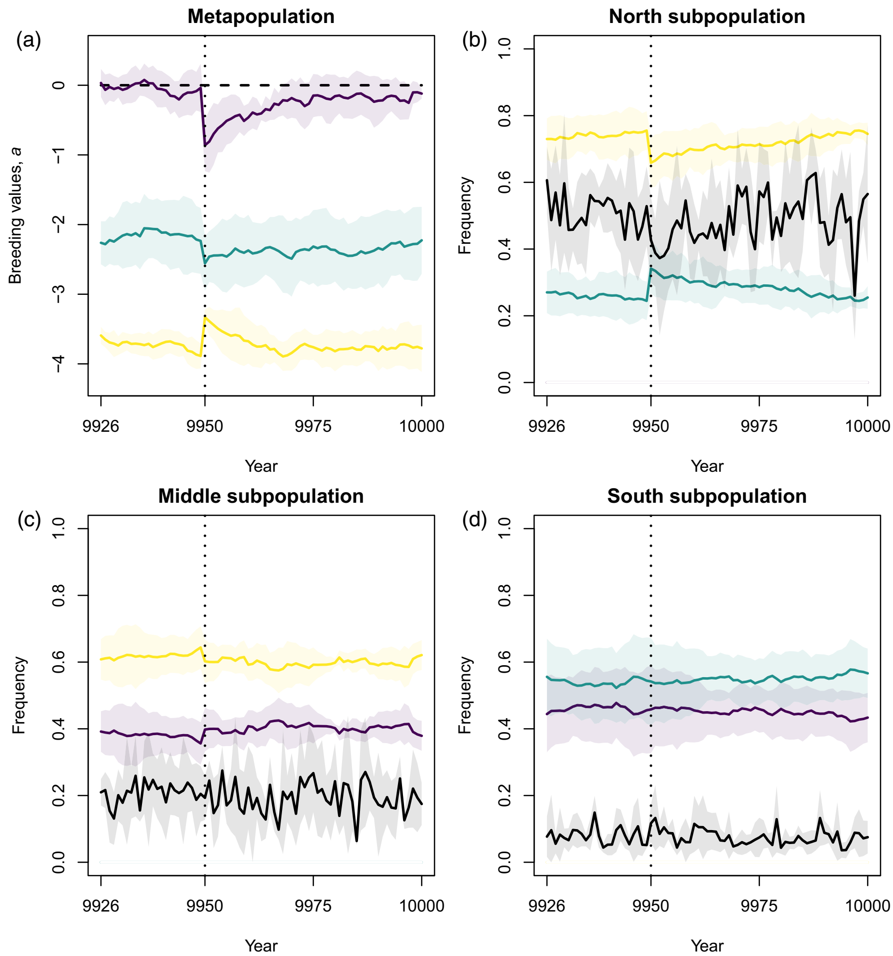

FIGURE 6 Evolutionary consequences of a non-breeding season extreme climatic event (ECE) striking the south site in year 9950 (vertical dotted lines), given a weak non-breeding season suitability gradient, $\gamma_n=\{1/2,1/3,1/5\}$ (as in Figure 5e). (a) Subpopulation mean breeding values across simulations (opaque bands show 95%CI) before and after the ECE. Purple, green and yellow show respectively north, middle and south subpopulation. (b–d): For each subpopulation (panel header), coloured lines show allele frequencies at destination locus, and black lines migrant frequencies. Lines show means and opaque bands 95% CI across simulations.

The point that local ECEs can induce spatio-seasonal eco-evolutionary dynamics extending far beyond the directly impacted site is further emphasized by considering larger PMMPs (e.g. with $S=5$ sites, Appendix S2). Here, an ECE impacting the southernmost site, which receives many immigrants from all subpopulations given a strong non-breeding season suitability gradient, causes strong population dynamic and evolutionary responses (the same three as observed above) in all subpopulations. If the migration cost m_c depends on distance travelled, more individuals from the northern subpopulations migrate to middle non-breeding season sites rather than the southernmost site. An ECE impacting the southernmost site then has slightly less impact on the breeding population size in the northernmost site than given $N=3$ sites, but ripple effects in both population and evolutionary dynamics throughout the entire PMMP still persist.

The differing timeframes of ecological and evolutionary responses following ECEs, manifested as different times for breeding and non-breeding season population densities to return to pre-ECE levels, also remained with lower fecundity ($f=2$ rather than 3) and hence reduced intrinsic population growth rate (Appendix S3). Alongside increasing population recovery times, reduced reproduction also slightly reduces the speed of evolution, thereby maintaining the discrepancy in recovery times for breeding versus non-breeding season population sizes.

4 | DISCUSSION

Eco-evolutionary responses of partially migratory metapopulations (PMMPs) to seasonal environmental variation will fundamentally depend on interlinked spatio-seasonal variation and evolution in vital rates. In PMMPs, the probability of seasonal migration effectively constitutes a vital rate because it directly causes variation in seasonal space use and resulting local population densities (Payo-Payo et al., 2022; Reid et al., 2018). Accordingly, our eco-evolutionary model examines interlinked dynamics of multiple subpopulations caused by non-breeding season sympatry stemming from evolving seasonal migration. It demonstrates how predictable and stochastic environmental variation can readily generate stable partial migration, and how local seasonal shocks (representing ECEs) can generate large-scale spatio-seasonal dynamics that affect the whole PMMP. We thereby highlight how eco-evolutionary dynamics in spatially structured and potentially migratory metapopulations can arise and be propagated in time and space.

4.1 | Evolution of stable PMMPs

Stable PMMPs readily evolved given sufficient among-site differences in non-breeding season conditions (formulated as differing density-dependence in mortality). These outcomes extend existing theoretical results on partial migration in two-patch systems (Griswold et al., 2010; Kaitala et al., 1993; Ohms et al., 2019), and show how differential migration, including combinations of partial and full migration or residence, can emerge from the same underlying genetic architecture. This matches broad-scale empirical patterns. For example, several bird species are partially migratory in western Europe (with milder winters) and fully migratory in eastern Europe (with colder winters, e.g. chiffchaff *Phylloscopus collybita*, white stork *Ardea circonia*, Spina et al., 2022). In our simulations, evolved PMMP-wide space use caused individuals to experience similar non-breeding season survival probabilities despite occupying sites of different density and suitability, approaching 'ideal free' migratory patterns, as reported in natural PMMPs (e.g. Japanese sea bass *Lateolabrax japonicus*, Kasai et al., 2018; elk *Cervus canadensis*, Martin et al., 2022). Our suitability gradients generated instances of both 'shared breeding' partially migratory subpopulations, and 'shared non-breeding' partial migration where fully resident subpopulations receive incoming migrants during non-breeding seasons (Griswold et al., 2010). With no (or very weak) gradients in non-breeding season conditions, fully resident metapopulations evolved. Such loss of migration is expected if climate, land-use or other forms of anthropogenic change allow previously (partially) migratory subpopulations to function in single sites all year (Shaw, 2016).

Partial migration also evolved given stochasticity in non-breeding season survival among sites and years, even without any gradient in mean conditions, by effectively spreading the risk of experiencing harsh local conditions (Figure 4a). This 'diversifying' bet-hedging mechanism (sensu Seger & Brockmann, 1987) also emerged without density-dependence in survival, if non-breeding season conditions were sufficiently unpredictable (moderately high $\sigma_{m,n}^2$) and uncorrelated among sites and years (Figure 4b). First stated by Cohen (1967), the point that stochasticity alone could drive partial migration has been largely omitted in later work, which focuses on non-breeding season density-dependence as a key mechanism (Kaitala et al., 1993; Taylor & Norris, 2007). This focus may reflect the critique that bet-hedging is incompatible with frequency-dependent evolutionarily stable strategy (ESS) models of partial migration, since residents can outcompete partially migrant bet-hedgers during benign conditions between unpredictable harsh years (Lundberg, 1987). Yet, work on natural (meta)populations often invokes diversifying bet-hedging, and genotype-level risk-spreading is also congruent with observations of migratory polyphenisms in insects (Menz et al., 2019), and variation in migratory destinations and orientation in passerines (Reilly & Reilly, 2009). In such cases, although (arithmetic) mean fitness may be similar across migratory destinations, bet-hedging is favoured because it decreases genotype-level fitness variance. This logic is similar to that regarding evolution of dispersal, where bet-hedging can increase dispersal because it decreases fitness correlations among related individuals (Grantham et al., 2016; Poethke et al., 2007). However, resulting system dynamics, including responses to seasonal ECEs, will differ dramatically depending on whether bet-hedging operates through permanent dispersal or reversible seasonal migration. Most pertinently, only with evolving seasonal migration can local non-breeding season ECEs ripple out to substantially affect both breeding and non-breeding season densities throughout the PMMP, such as we demonstrate (Figures 5 and 6).

In contrast to non-breeding season conditions, spatial variation in breeding season conditions did not drive partial migration in our current model. This is partly because we did not let dispersal evolve, meaning that individuals experiencing relatively poor breeding season conditions cannot leave. Future studies should therefore consider co-evolution of seasonal migration and dispersal, including where density-dependent dispersal can produce ideal free breeding season distributions (i.e. subpopulation sizes; Cantrell et al., 2012; Hendrickx et al., 2013). Correlations between dispersal and seasonal migration could plausibly be positive (e.g. because they depend on the same locomotory system) or negative (e.g. because dispersing to year-round suitable locations eliminates need for subsequent seasonal migration, or because bet-hedging via one mechanism decreases benefits of bet-hedging through the other) (Cote et al., 2017; Tittler et al., 2009; Winkler, 2005). Further empirical and theoretical studies are required to evaluate the form, basis and implications of such associations. However, individuals within well-studied PMMPs are highly reproductively philopatric, despite consistent differences among sites in breeding season conditions (e.g. European shags *Gulosus aristotelis*, Barlow et al., 2013; Eurasian oystercatchers *Haematopus ostralegus*, Allen et al., 2019), implying that dispersal is not a driving force of system dynamics occurring on the spatial scale of seasonal migration. Instead, differences in breeding season survival may cause more subtle eco-evolutionary effects. For example, in our model, higher breeding season mortality decreased expected lifespan, but increased per capita reproductive success, because juvenile recruitment is density-dependent and more 'slots' for offspring are available if fewer adults survive. Resulting local adaptation of life history could affect whether evolved migratory strategies reflect bet-hedging, if alternative strategies differ in their fitness variance in stochastic environments (e.g. Starrfelt & Kokko, 2012).

4.2 | Reponses to extreme climatic events (ECEs)

Our simulations highlight how major demographic perturbations caused by a single local ECE can cause far-reaching eco-evolutionary effects that extend throughout PMMPs. While local breeding population sizes typically recovered relatively fast, impacts on non-breeding season populations persisted over longer timeframes, often several decades. These outcomes result from simultaneous strong ECE-induced selection against residence in the subpopulation breeding at the perturbed site and selection against migration in other subpopulations from which incoming seasonal migrants into the perturbed site originated, generating spatially divergent selection. Resulting evolutionary changes caused long-lasting effects, since further evolutionary changes in both liability to migrate and

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destination allele frequencies are required for the PMMP to return to its pre-perturbation equilibrium non-breeding season distribution. Such protracted periods away from system equilibrium following ECEs, alongside any environmentally induced variation in liability to migrate, may help explain the lack of balanced fitness effects evident in an empirical meta-analysis of populations with alternative migratory tactics (Buchan et al., 2020).

Seasonal environmental perturbations causing up to 80% local mortality have been documented in several partially migratory systems, including European shags *Gulosus aristotelis* during extreme winter storms (Acker, Burthe, et al., 2021; Frederiksen et al., 2008), greater flamingos *Phoenicopterus roseus* during extremely cold winters or local toxic cyanobacterial blooms (Alonso-Andicoberry et al., 2002; Sanz-Aguilar et al., 2012), and bighorn sheep *Ovis canadensis* during disease epidemics (George et al., 2008, although transmissible diseases have further epidemiological consequences for metapopulation dynamics; Balstad et al., 2021). At least some responses arising from our simulated perturbations also occur in natural PMMPs. For example, after extreme winter storms, a European shag population became detectably more migratory, because survival selection against residents increased mean liability values (Acker et al., 2023). Intermittent ECEs could consequently help maintain partial migration, given reproductive selection favouring residence (Acker, Burthe, et al., 2021). Given that eco-evolutionary responses to weaker or more spatially restricted ECEs will be mechanistically similar (but with smaller effects), there is a strong empirical basis from which to postulate that the types of eco-evolutionary dynamics captured by our current model, including impacts of ECEs, could widely occur in nature.

4.3 | Implications and future advances

Our general and flexible model formulation allows capturing diverse PMMP structures and impacts of different ECE frequencies, spatial scales and durations. While our current parameterizations and simulations are designed to highlight general principles rather than envisaging any particular system, key parameters can in principle be explicitly estimated from field data. In particular, the quantitative genetic threshold trait formulation has a well-developed conceptual, statistical and empirical basis (Dodson et al., 2013; Pulido, 2011; Reid & Acker, 2022; Roff, 1996), allowing estimation of additive genetic variance in liability to migrate alongside various environmental effects and seasonal selection (Acker et al., 2023; Acker, Burthe, et al., 2021). Parameterizing and analysing eco-evolutionary models of real PMMPs is consequently increasingly tractable, especially by coupling tracking technologies with life-history and genetic data. This contrasts with much previous theory on evolution of partial migration, dispersal and other dichotomous traits, which typically models probabilities of employing alternative tactics and/or evolutionarily stable equilibria, which are less directly empirically tractable. A remaining empirical challenge is then to estimate strengths and shapes of density-dependence in seasonal vital rates (Thorson et al., 2015) and in liability to migrate (Hovestadt et al., 2010), which are key parameters in our and previous partial migration models. As our simulations reveal that spatio-temporal environmental variation in liability components can cause strong fitness differences among residents and migrants within and between years (Appendix S1), relatively long-term field studies will be required for accurate inference.

Our model could be extended to incorporate further consequences of migratory polyphenisms, including (dis)assortative mating, further forms of plasticity, and carry-over effects of migration phenotype on subsequent territory acquisition, dispersal propensity, and/or reproductive success (as previously observed or postulated; Acker, Burthe, et al., 2021; Kokko, 2011; Morinay et al., 2024; Shaw & Levin, 2011). Interestingly, many partially migratory species show substantial permanent individual effects on migration, with between-year adult repeatabilities reaching 70%–90% (Arnekleiv et al., 2022; Chambon et al., 2019; Grist et al., 2014; Martin et al., 2022). Such effects, which likely primarily represent developmental plasticity, could exacerbate the magnitude and duration of ECE impacts on PMMP composition and dynamics, especially in long-lived species. Episodes of strong selection that remove residents or migrants will then cause persistent shifts in phenotype frequencies due to phenotypic inertia alongside microevolutionary change (Acker et al., 2023). Thus, incorporating variation in among- and within-individual phenotypic plasticity will facilitate full understanding of joint population dynamic and microevolutionary responses of natural PMMPs to dramatically changing spatio-seasonal environmental conditions.

AUTHOR CONTRIBUTIONS

Thomas R. Haaland and Jane M. Reid conceived the objectives. Thomas R. Haaland built and analysed the model with input from Jane M. Reid, Ana Payo-Payo, Paul Acker and Irja I. Ratikainen. Thomas R. Haaland wrote the manuscript with input from Jane M. Reid. All authors contributed to conceptual development, manuscript editing and presentation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code is available from Dryad Digital Repository https://doi.org/10.5061/dryad.1rn8pk12n (Haaland et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Baseline model scenarios and variations.

Appendix S2: Movement and metapopulation evolution in larger landscapes.

Appendix S3: Effects of ECEs when fecundity is lower.

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