

Patch spatial attributes and time to disturbance affect the emergence of source local populations within ephemeral habitats

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ABSTRACT

Understanding the demography of local populations within ephemeral habitat patches is crucial for effective local (site-based) conservation management in spatially and temporally heterogeneous environments. Evidence suggests that species persisting in networks of ephemeral patches often exhibit source-sink dynamics, where certain local populations act as temporary sources at some time between initial colonization and patch disappearance due to disturbance. Here we present an individual-based demographic model inspired by Cabrera voles (*Microtus cabreræ*) in dynamic agricultural mosaics to test the hypothesis that the emergence of a source local population within an ephemeral habitat patch is largely driven by the combined effects of the patch spatial attributes (size, internal quality and connectivity to other hypothetical patches) and the time to disturbance (i.e. the patch lifespan). We focused on two key emergent demographic metrics quantifying the source-sink status of local populations based on their self-sustainability and potential contribution to other patches. We used sensitivity analyses to estimate the strength of linear associations between these metrics and the patch spatial attributes, and to quantify the main and interaction effects across different patch lifespans since initial colonization. Our model revealed that considerable spatial and temporal variation may emerge in local populations' source-sink status based on differences in patch size, internal quality, connectivity, and lifespan. According to predictions, patch internal quality correlated positively with local population self-sustainability and potential contribution to other patches, though the strength of these relationships was mostly relevant only after about three vole generation times (ca. one year) since initial colonization, and only in combination with the positive effects of patch size and connectivity. Accordingly, results also supported the prediction that the emergence of a temporary source local population is conditional to the longevity of the habitat patch, with short patch lifespans (less than about three vole generation times) greatly limiting local population self-sustainability and potential contribution to other patches. While empirical testing is needed to confirm these findings, our study strengthens the view that local management efforts focusing on reducing or mitigating disturbance (e.g. severe droughts, human farming activities) at large and well-connected high-quality patches will likely promote the occurrence of temporary source local populations, which should be crucial for long-term species persistence over larger spatial scales.

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1. Introduction

All environments vary in space and time, and many species have adapted to persist in dynamic ecosystems where suitable habitat is patchily distributed and exposed to natural and anthropogenic disturbance (e.g. Amarasekare and Possingham, 2001; Freemark et al., 2002; Keymer et al., 2000; Reigada et al., 2015; Van Teeffelen et al., 2012). Illustrative examples include fire-prone ecosystems (e.g. forests, savannas), areas affected by severe water imbalances (e.g. grasslands in arid and semi-arid environments), or by repeated drought or flood events (intermittent wetlands), as well as agricultural areas impacted by harvesting, grazing and mowing, all contributing to create spatial and temporal patterns in habitat structure and composition. Disturbance-driven variation in the amount, location and configuration of suitable habitat critically affects species that persist via extinction-colonization dynamics, altering population states and trajectories from the local (patch-level) to the landscape scale (e.g. Amarasekare and Nisbet, 2001; Butterworth et al., 2023; Heinrichs et al., 2016; Johnson, 2004; Reigada et al., 2015). Empirical and modelling studies indicate that species inhabiting networks of short-lived habitat patches (e.g. early successional grasslands created and destroyed through disturbance) often persist through source-sink dynamics, whereby local populations with net demographic deficits are supported by immigration from local populations with net demographic excess (e.g. Frouz and Kindlmann, 2015; Reigada et al., 2015). This suggests that the long-term persistence of such species may critically depend on the continued (though possibly fluctuating) availability of patches that, once colonized, can potentially behave as temporary demographic sources. Identifying the specific attributes of local habitat patches that enhance their potential to become temporary sources within a few generations of being colonized is therefore important to improve conservation management in dynamic environments (e.g. Furrer and Pasinelli, 2016; Sample et al., 2019). This is, however, hindered by the difficulty of identifying the source-sink status of local populations subjected to short-term (transient) dynamics, in which sharp temporal changes in key demographic parameters may occur over time between initial colonization and patch disappearance due to disturbance (e.g. Johnson, 2004; Paquet et al., 2020).

Two major demographic properties are commonly used to identify the source and sink status of local populations: self-sustainability (i.e. the ability to persist through local recruitment from births), and demographic contribution to other patches (i.e. the disproportionate production of propagules beyond patch boundaries relative to those absorbed) (Loreau et al., 2013; Pulliam, 1988; Runge et al., 2006). Evaluating the self-sustainability of persisting local populations at any given time involves examining the imbalance between births and immigration. When local recruitment from births (internal recruitment) is too low to surpass mortality or emigration, then population persistence will be highly dependent on immigration (external recruitment), otherwise it will face local extinction (Hanski and Gaggiotti, 2004; Millon et al., 2019). Evaluating the demographic contribution of a local population to other patches requires assessing the asymmetries in directional flow between immigration and emigration (Loreau et al., 2013; Runge et al., 2006). If the flux of individuals favours immigration over emigration, then the local population may be considered a sink. Conversely, if local population persistence is guaranteed by internal recruitment through births, and the outflow of emigrants outweighs the influx of immigrants, then the local population will qualify as a source (e.g. Altermatt and Ebert, 2010). While the determination of the source-sink status of occupied habitat patches is usually made under the assumption of long-term equilibrium dynamics (but see Sample et al., 2020), efforts to measure the short-term (transient) self-sustainability and potential demographic contribution of newly established local populations in ephemeral patches remains elusive (e.g. Caswell, 2007; Heinrichs et al., 2019). However, given that many species live in dynamic environments characterized by transient short-lived habitat

patches where local populations frequently operate below equilibrium, understanding how patch spatial attributes and time to disturbance influence the emergence of a temporary source is important for ecological and conservation research (Caswell, 2007; Ezard et al., 2010; Iles et al., 2018).

Variation in habitat quality has been at the core of source-sink dynamics since the concept was first introduced, wherein high-quality habitats function as sources, while low-quality habitats function as sinks (Pulliam, 1988). However, there is still limited understanding of whether variation in other local patch attributes (e.g. size, connectivity) also shapes the emergence of sources and sinks, and how patch lifespan impacts post-colonization sink-to-source transition potential (e.g. Altermatt and Ebert, 2010; Heinrichs et al., 2016; Pasinelli et al., 2011). Notably, it is still largely uncertain how variations in patch size, intrinsic quality, and connectivity interact in determining the potential of local populations to, at least temporarily, become self-sustainable and able to positively contribute to an overall metapopulation before facing local extinction due to disturbance. This is probably related to the difficulty of tracking the required amount of detailed demographic and individual level data spanning the patches' lifespan since initial colonization, particularly when considering the large number of suitably different patches which would be required to gain inference into such processes (e.g. Heinrichs et al., 2019, 2016; Runge et al., 2006).

Because local demography emerges from a complex interaction between individuals within patches of varying characteristics, process-based approaches incorporating complex biological data are increasingly recommended and used to generate new insights and predictions on the way complex systems may respond to environmental change (e.g. Pilowsky et al., 2022; Poniatowski et al., 2018). In particular, Individual-Based-Models (IBMs, Grimm and Railsback, 2005) have an enormous potential for recreating the demographic dynamics of small, recently formed local populations, and the appearance of complex responses to patch size, quality and connectivity (DeAngelis and Grimm, 2014; Grimm et al., 2017). IBMs have at times been deemed over-parameterized compared to more simplified/cruiser caricature models (Kaul and Ventikos, 2013). However, where sufficient biological knowledge is available to motivate the inclusion of processes in a model caricature, and sufficient data is available to parameterise functional relationships, IBMs allow for a highly suited synthesis of a broad range of knowledge that can result in emergent properties that are difficult to identify in nature (Kaul and Ventikos, 2013; Railsback and Grimm, 2019; Wilensky and Rand, 2015).

Here, we developed an *in silico* IBM approach inspired by the near-threatened, but data-rich, Iberian endemic Cabrera vole (*Microtus cabrerarum*) in Mediterranean farmland, to test the general hypothesis that the emergence of a source local population within an ephemeral habitat patch is largely driven by the combined effects of patch spatial attributes (including its size, internal quality and connectivity) and the time to disturbance (i.e. the patch lifespan) (e.g. Fahrig, 1992). Based on simulations quantifying local population internal recruitment from births, immigration inflow, and emigration outflow at different times since initial colonization, we explore how patch characteristics affected emergent demographic imbalances determining the source-sink status of local populations. We predict that internal patch quality should be the most critical spatial attribute driving local population self-sustainability and demographic contribution beyond patch boundaries, due to its general positive association to reproduction and local recruitment (e.g. Griffen and Norelli, 2015). However, complex synergistic interactions among patch spatial attributes may come into play, in response to the temporal changes in local population density over time since colonization (Hatton, 2020; Santoro et al., 2016). For instance, as density increases over time within large and well-connected patches, and local living space becomes limited, the relevance of immigration should gradually decrease relative to internal recruitment from births and to the outflow of emigrants, potentially involving a transition of the local population from sink to source (Pulliam and Danielson, 1991).

Therefore, we also predict that, in general, shorter patch lifespans (e.g. due to increased habitat turnover or frequency of disturbance) should weaken the emergence of source local populations, as there may be limited time to approach local carrying capacity or near-equilibrium density (Heinrichs et al., 2016; Van Teeffelen et al., 2012).

2. Material and methods

2.1. Model species

Cabrera voles are considered habitat specialists occurring in wet grassland habitat patches that are typically scattered across Mediterranean agricultural landscapes, and are often associated to small streams, soil depressions, temporally flooded or waterlogged areas, or wet meadows along the margins of agricultural fields and roads (Pita et al., 2014). Within these patches, Cabrera voles are typically organised in small family groups consisting of a monogamous breeding pair and their offspring (Pita et al., 2010), preferring microhabitats that offer dense cover by sedges and rushes, which provide food and protection against predators and extreme temperatures (e.g. Luque-Larena and López, 2007; Pita et al., 2011, R. 2006). Mean generation time is estimated at ca. 4 months, corresponding to around 3 generations per year (Mathias et al., 2023). In intensive Mediterranean farmland, suitable habitat patches rarely exceed 2000m² and are subjected to frequent turnover due to human activities (e.g. ploughing, overgrazing) with many patches often lasting no more than about two years, eventually recovering some time after the disturbance (Pita et al., 2007). Because the species seems to be relatively well-adapted to such habitat dynamism, it is likely that some patches may behave as temporary sources along their relatively short lifetime, making the identification of the factors determining the occurrence of such sources an important goal in local conservation management. At present, the species is threatened by changes in land-uses associated to agriculture intensification, and abandonment of traditional agricultural practices, which result in the loss, fragmentation and degradation of suitable habitats (Pita et al., 2014; Mathias et al., 2023). These threats, together with climate change, have been identified as the main factors responsible for the predicted population declines of Cabrera vole (meta)populations in many areas across its distribution range (Garrido-García et al., 2018; Mestre et al., 2015). The species thus provides a suitable model for other species with both metapopulation dynamics and small group sizes constrained by short-lived habitat patches.

2.2. Model description

We developed an individual-based modelling (IBM) framework implemented in NetLogo (version 6.2.1, Wilensky, 1999) to simulate the post-colonization demography of the Cabrera vole within a single short-lived habitat patch amid a hostile matrix. The model consisted in repeated simulations considering different combinations of patch size, internal quality and connectivity to other hypothetical patches (not explicitly represented) in order to uncover the site-specific spatial attributes under which a local population in a newly colonized habitat patch may, at least temporarily, transition from sink to source. Below, we provide a general overview of the model's overall structure and processes involved, following the ODD protocol (Overview, Design concepts, Details) as recommended by Grimm et al. (2020). For a full ODD model description (Grimm et al., 2020, 2010; V. 2006); see Supporting information, section 'Detailed ODD protocol'. All simulation runs for testing and analysing the model, were performed using the "nlrx" package (version 0.4.3, Salecker et al., 2019) for program R (version 4.1.1, R Core Team, 2021). The full model code is available at: https://github.com/TCrispimMendes/IBM_Emergence_Of_Source_Local_Populations_Within_Ephemeral_Habitats

The overall purpose of our model was to simulate individual-level processes and to assess the role of patch spatial attributes and time to

disturbance in emergent demographic parameters and metrics quantifying local population self-sustainability and contribution to other patches. For this, the model systematically considered multiple combinations of patch size, internal quality, and connectivity values, with corresponding patch attributes defined for each simulated population during model initialization and remaining constant throughout the simulation. Patch size varied from 500 m² to 5000 m², reflecting the typical range of patch sizes occupied by the species in fragmented landscapes (Pita et al., 2014). Patch internal quality and connectivity were formulated as single synthetic measures ranging from 0 (minimum) to 1 (maximum), implicitly reflecting different biotic and abiotic conditions affecting habitat suitability at the patch (e.g. vegetation and soil properties) and landscape scales (e.g. proximity to surrounding habitat patches and degree of matrix hostility).

We adopted a pattern-oriented modeling (POM) strategy (Grimm, 2005; Grimm and Railsback, 2012) in order to align model outcomes to empirical data on individual-level patterns and behaviors, including spatial organization, breeding behavior, parental care, migration, and survival. The model processes and sequence of events are illustrated in Fig. 1.

The model includes the following entities: habitat cells ($1 \times 1\text{m}^2$), Cabrera vole individuals (*agents*), and the global environment (*observer*; the only entity at the system level, controlling the sub-models [see Supporting information, Section 'Detailed ODD protocol'] and defining the simulation date). The state variables characterizing these entities are listed in Table 1. Habitat cells are arranged in a circular pattern around the center of the model world, forming a single habitat patch, varying in size according to the number of cells included in the simulation, which determine patch carrying capacity. Each Cabrera vole individual (except nestling pups) is represented by a circular home range, with size randomly generated according to a normal distribution $N(X, \sigma)$ of $N(535.64, 327.29)$ for males, and $N(355.45, 271.39)$ for females, following Pita et al. (2010). The spatial arrangement of individuals within the patch followed the prevailing monogamous mating system of the species, adhering to home-range overlapping rules based on individuals' sex, relationship type (e.g. mates vs. non-mates), kinship, and current breeding status (Pita et al., 2010) (see Supporting information, Section 'Detailed ODD protocol', Table S5).

Each simulation was conducted over a period of two years (approximately six vole generation times), with a single time step in the model representing one week. This weekly time scale is adequate for accurately capturing individual behaviors and post-colonization demography of the species, while the two-year duration corresponds to the typical lifespan of patches found in highly managed farmland areas (e.g. Pita et al., 2007). Simulations were initiated at the beginning of October, coinciding with the period of increased reproductive investment (Pita et al., 2014; Ventura et al., 1998). Each simulation initiated with one male and one female founding voles, representing a recent colonization event in the patch.

At each time step, relevant processes included maternal nest leaving and territory searching (at 6 weeks of age), reproductive maturation (at 8 weeks of age), and mate searching (for adults without a defined mate, and excluding parents and full siblings to avoid inbreeding, e.g. Lambin, 1994). In addition, individual probabilities of survival, reproduction, emigration and immigration were determined according to empirical information on species biology and ecology (Fernández-Salvador et al., 2005a, 2001; Pita et al., 2010; Proença-Ferreira et al., 2019). Specifically, weekly probability of mortality was generated for each animal at each time step based on Bernoulli trials with probability of 0.12 for juveniles and 0.02 for adults (estimated from Fernández-Salvador et al., 2005b; Radchuk et al., 2016; Topping et al., 2012) (see Supporting Information, Section 'Detailed ODD protocol', Section 5 and 7.10).

Regarding reproduction probability, although Cabrera voles can mate throughout the year, the probability of successful breeding typically fluctuates according to seasonal variations in local habitat quality (Fernández-Salvador et al., 2005b, 2005a; Rosário, 2012; Ventura et al.,

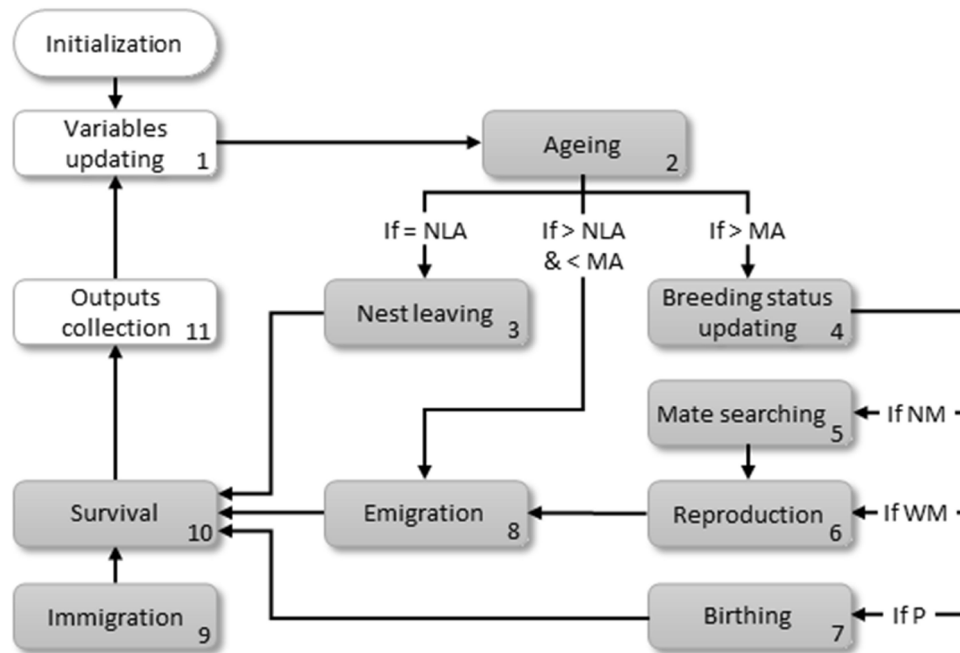


Fig. 1. Conceptual diagram of the model to simulate post-colonization demography of Cabrera voles within a short-lived habitat patch amid a hostile matrix, considering different combinations of patch size, internal quality and connectivity. White boxes correspond to processes at the system level (i.e. the environment and data collection) and grey boxes correspond to processes at agent level (i.e. the voles). The numbers in the lower right corner of the boxes refer to the submodel corresponding to the respective process (see Supporting information, section “Detailed ODD protocol”). Some processes are dependent on the age of the individuals: maternal nest leaving age (NLA) and maturation age (MA); or breeding status: no mate (NM), with mate (WM) and pregnant (P).

Table 1

List of agents intervening in the model, with their state variables and corresponding status or measure unit. * indicates female-specific state variables.

State Variable	Variable type (possible values)
Habitat cells	
Cell location	Numeric (spatial coordinates)
Habitat type	Categorical (“favourable”; “matrix”)
Cabrera voles	
Unique identification code	Numeric (-)
Location in patch	Numeric (spatial coordinates)
Sex	Categorical (“F”; “M”)
Age	Numeric (weeks)
Residence time in the patch	Numeric (weeks)
Home-range size	Numeric (m ²)
Breeding status	Categorical (Mate’s ID; “no-mate”; “helper”)
Parent’s identification codes	Categorical (Parent’s ID; “founder”; “immigrant”)
Time step of last reproduction*	Numeric (-)
Female is pregnant	Boolean
Litter’s father identification code*	Numeric (-)
Time step to give birth*	Numeric (-)
Global environment	
Date at the end of the current time step	Date (day/month/year)

1998) Therefore, weekly probability of reproduction were generated for each individual by Bernoulli trials with probabilities randomly taken from the range of variation identified by empirical observations across different months of the year (between 0 and 100 %, estimated from Fernández-Salvador et al. 2005b; Rosário 2012), weighted by the patch internal quality (e.g. Griffen and Norelli, 2015) (see Supporting Information, Section ‘Detailed ODD protocol’, Section 5 and 7.6). As for inter-birth intervals, while postpartum mating behaviour of Cabrera voles remains undocumented, females were allowed to give birth only once the previous litter had vacated the nest. Although most vole species

can mate and give birth within less than ca. 30 days postpartum (Gilbert, 1984), we assumed limited female receptivity during lactation, beginning at postpartum oestrus, given the Cabrera vole is considered a less prolific, slow-reproducing species, with k-strategic life-history characteristics (investment in offspring via parental care) (Fernández-Salvador et al., 2005b). This conservative assumption was also supported by the association of the species to small patches of scarce habitats, which may also delay postpartum mating, owing to resource shortage, as found in other *Microtus* species (e.g. Sabau and Ferkin, 2013).

The weekly probability of emigration of lactating females or pair-bounded breeding animals was set at 0 %, while individuals unable to establish a home-range due to space limitations had an emigration probability of 100 %. Remaining animals were assigned a probability of emigration based on Bernoulli trials with probability taken from the range of empirical values found in natural populations (between 7.5 and 17.7 %, estimated from Fernández-Salvador et al. 2005b; Proença-Ferreira et al. 2019), weighted by the patch connectivity value (see Supporting Information, Section ‘Detailed ODD protocol’, subsection 7.1). These rules were implemented to reflect the individuals’ propensity to emigrate, while considering the socio-ecological context and the proximity to putative neighbouring patches, in line with empirical data and general ecological theory (e.g. Hanski and Gaggiotti, 2004), thus providing realism to our model. The overall emigration probability at each time step thus emerged from individuals’ responses to competition for space and for mates, both largely regulated by density-regulated stochastic process.

The weekly probability of immigration of a new individual into the focal patch was generated based on Bernoulli trials with probability randomly taken from the range of variation identified in empirical observations across the annual cycle (between 5.0 and 37.6 %, estimated from Pita et al. 2007; Proença-Ferreira et al. 2019), weighted by the patch connectivity value (e.g. Hanski and Gaggiotti, 2004) (see Supporting Information, Section ‘Detailed ODD protocol’, subsections 6 and 7). However, successful settlement of immigrants ultimately depended on space availability for establishing a home range while adhering to the

spatial overlapping rules considered (see Supporting information, Section ‘Detailed ODD protocol’, subsections 7.3).

Overall, the fundamental concepts underlying the design of the model thus support the main requirements that i) Cabrera’s vole populations are patchily distributed, with individuals typically grouped into distinct local populations restricted to small habitat patches (R. Pita et al., 2006; Rosário and Mathias, 2007); ii) reproduction follows a *k*-selection strategy (Fernández-Salvador et al., 2001), where monogamy stands as the prevailing social and mating system, even though eventual deviations to facultative polygyny were also deemed possible (Pita et al., 2014); iii) breeding activity follows an opportunistic strategy linked to variations in local habitat quality (Fernández-Salvador et al., 2005b); and iv) migration occurs in response to competition for mates and space. These principles are represented in the model through the different submodels for reproduction, socio-spatial overlapping rules among individuals, and migration (see Supporting information, Section ‘Detailed ODD protocol’).

2.3. Model outputs

The model was designed to collect demographic data at three months intervals, roughly corresponding to the end of the four main seasons in the Mediterranean basin (autumn, from October to December; winter, from January to March; spring, from April to June; and summer, from July to September). This allowed us not only to capture eventual transitions in population source-sink behaviour over time, but also to infer the status of local populations at different hypothetical disturbance timings (from 3 months to two years). According to our hypothesis, the primary outputs emerging from our model focused on metrics describing the strength of local populations’ self-sustainability and potential contribution to other patches. Several metrics with varying emphasis on self-sustainability and demographic contribution, have been suggested to differentiate sources and sinks or to rank the relative importance of local populations based on various key demographic parameters (e.g. births, mortality, immigration and emigration rates) (e.g. Pulliam, 1988; Runge et al., 2006; Sample et al., 2019). However, these metrics have been specifically applied for populations in equilibrium, while their utility remains uncertain under transient dynamics (Sample et al., 2020). In addition, the use of single metrics that accurately reflect both self-sustainability and potential demographic contribution of local populations remains contentious (Runge et al., 2006; Sample et al., 2020), and different metrics may therefore be required for assessing the changes in source-sink status of local populations. In particular, because the source-sink status of local populations can change depending on the environmental conditions, there is little prospect of devising a single measure of the intrinsic strength of sources and sinks (Loreau et al., 2013). Therefore, here we opted to infer on the source-sink status of local populations based on two simple metrics that can be extracted for relatively short-interval time periods along transient population dynamics. Specifically, we measured the imbalance between births and immigration (hereafter, B-I index) in persisting local populations (i.e. where overall recruitment apparently compensates deaths) calculated as the difference between net births and net immigration divided by the total number of recruits every three months (see Table 2). This index measures the role of births and immigration in overall local population growth, varying between -1 and 1. Positive values in the B-I index indicate a higher proportion of births over immigration (i.e., self-sustaining through reproduction), with negative values indicating the opposite pattern (i.e. persistence via immigration). We also quantified the imbalance between immigration and emigration (hereafter I-E index) as the difference between the number of immigrants and the number of emigrants divided by the total number of migrants every three months (e.g. Christensen and Walters, 2004; Stoffels et al., 2016), see Table 2). This index considers the number of emigrants leaving the patch independently of their survival and ability to reach and establish in a new patch, varying also between -1 and 1, with positive values

Table 2
List of emergent demographic outputs extracted from the model every 3 month-intervals, roughly corresponding to 4 main seasons in the Mediterranean basin (autumn, winter, spring, and summer).

Output	Description
Inference	
B-I index	Net balance between local recruitment and immigration, calculated as: $(N_{\text{Births}} - N_{\text{Immigrants}}) / (N_{\text{Births}} + N_{\text{Immigrants}})$
I-E index	Net balance between immigration and emigration, calculated as: $(N_{\text{Immigrants}} - N_{\text{Emigrants}}) / (N_{\text{Immigrants}} + N_{\text{Emigrants}})$
Validation	
Extinction	Whether the local population extinction occurred (1) or not (0)
Density	Snapshot of local population density (individuals/ha)
Sex-ratio	Snapshot of sex-ratio (proportion of males) in the local populations, calculated as: $(N_{\text{Males}}) / (N_{\text{Females}} + N_{\text{Males}})$
Residency	Snapshot of mean individual residence times in the local populations (in weeks)

indicating higher net immigration (hence limited demographic contribution to other patches) and negative values indicating higher net emigration (i.e. increased demographic contribution). In addition, we also investigated other emergent demographic parameters (densities, sex-ratios, extinction rates) for model validation purposes (Table 2).

2.4. Model validation

Model verification and quality assurance were carried out at different levels. First, while writing the code, the syntax was checked using the NetLogo’s built-in debugger. Then, a visual debugging of the running model was performed using the NetLogo visual interface.

To test the performance of the model, a pattern-oriented validation (Grimm, 2005; Grimm and Railsback, 2012) was conducted using patterns recorded in the literature based on real-world populations (e.g. Wang, 2013) regarding (i) extinction rates (Pita et al., 2007), (ii) density (Fernández-Salvador et al., 2005b; Landete-Castillejos et al., 2000; Peralta et al., 2023; Sabino-Marques et al., 2018), (iii) sex-ratio (Pita et al., 2014), and (iv) residence times (Fernández-Salvador et al., 2005b) (Table 2). We assumed that overlapping uncertainty boundaries between simulation and empirical data would provide evidence that the simulation was adequate for calculating the demographic indexes used to infer on source-sink strength of local populations. For this step of model validation, we used a Latin hypercube sample procedure, in “nlrx” (Salecker et al., 2019), to generate 250 parameterizations over the ranges of each input parameter (size, quality and connectivity). We then ran these parameterizations with 10 different random-seeds (making a total of 2500 runs) to account for model stochasticity.

In addition, we also assessed whether some of the validation outputs changed as predicted according to the variation in patch attributes, and considering the transient nature of local population dynamics. For this, we fitted single-variable linear regression models with Normal distributed errors, using the data derived from the Sobol estimator simulations (described below). Specifically, we checked whether, despite the considerable variability, there was a positive trend in density estimates over time in established local populations, driven by the progressive occupation of empty space (through local recruitment and immigration) since initial colonization towards carrying capacity. Similarly, we examined whether our model captured a decrease in demographic extinction rate as patch size, connectivity and habitat quality increased, and whether local density increased with habitat quality, as expected from well-established ecological theory (e.g. Hanski and Gaggiotti, 2004). While we assumed that the interactions between the patch spatial attributes would have larger effects on vole demography than the main effects (potentially leading to limited explained variance by single-variable linear regressions), this approach was mostly oriented to assess the coefficients’ sign (either positive or negative), rather than their magnitude or predictive ability.

2.5. Sensitivity analyses of model outputs

We conducted a global sensitivity analysis to check the robustness of the IBM outputs, focusing on those parameters directly related to our main hypotheses. For this, we used two methods; one based on linear regression and another on the decomposition of functional variance of each model response for each combination of patch size, quality and connectivity values. These methods measure two different model properties. In the case of linear regression, we used the Latin hypercube sampling partial rank correlation coefficients (LHS-PRCC). This method provides a non-parametric measure of the strength, direction and statistical significance of monotonic associations between model outputs and each patch attribute, after the removal of the linear effects of the other attributes (Marino et al., 2008). The PRCC ranges from -1 to $+1$, where values near 0 signify the absence of linear relationships, while those closer to -1 or 1 denote perfect negative or positive linear correlations, respectively. By leveraging this method, we can effectively rank patch attributes based on their impact on each model output. For decomposing variance, we used Sobol's method, which allows the decomposition of model outputs' variance into variances attributable to each patch attribute, distinguishing and quantifying the contribution of their direct and interaction effects (Sobol, 1993). The Sobol' method does not use fitted functions, but instead decomposes the variance based directly on a sample from the parameter space (Saltelli et al., 2008). Because the method aims to quantify the output variability based on this variance decomposition, it is not intended to identify the cause of the input variability, but rather to indicate the extent of its impact on model outputs (ten Broeke et al., 2016). Sobol indices range from 0 to 1 , with values nearing 0 indicating a negligible contribution of the corresponding variable to model output variability, while values close to 1 imply significant influence. When a model output is highly sensitive to a particular parameter, the parameter is considered a key-player in regulating that output.

For the implementation of the LHS-PRCC, the full ranges of each input parameter (size, quality and connectivity) were used to generate 500 parameterizations in "nlrx" R package (Salecker et al., 2019), which was run with two different random-seeds (making a total of 1000 runs) to account for model stochasticity. The results were then used to determine the partial-rank correlation coefficients and corresponding 95 % confidence intervals (via 100 bootstrapped samples) for each parameter, using the "sensitivity" R package (Iooss et al., 2019). Parameters were considered influential if 95 % confidence intervals of correlation coefficients did not overlap 0 .

In the case of Sobol's method, we calculated two main sensitivity indices for each parameter: first-order sensitivity index (S_i), and a total-order sensitivity index (S_{Ti}). S_i estimates the effect of each input parameter on each given model output, without considering the interaction effects among parameters. Conversely, S_{Ti} measures the full contribution of a single parameter to each model output while also considering possible nonlinear interactions among input parameters (Homma and Saltelli, 1996). In order to fully understand the interactions amongst input parameters, we also calculate the second-order (S_{ij}) and third-order (S_{ijk}) Sobol's indices, which measure the interaction effect between two and among three parameter arrangements respectively, on each model output (Saltelli et al., 2008).

Sobol's sensitivity indices were computed using Monte Carlo estimation implemented in "nlrx" (Salecker et al., 2019). The first, second and third-order indices were computed using the original estimator of Sobol (Sobol, 1993), whereas the total-order indices were computed using the Sobol-Jansen estimator (Jansen, 1999; Saltelli et al., 2010). The computational cost of these estimators depends on the number of input parameters (p) and the size of the Monte Carlo sample matrix (n), at a total cost of $(p + 2) \times n$, in the case of Sobol-Jansen estimator. In the case of the original Sobol estimator, the computational cost also depends on the number of indices to estimate (N), at a total cost of $(N + 1) \times n$.

For this analysis, we chose to use 2000 Monte Carlo samples, corresponding to a computational cost of 20,000 runs for Sobol-Jansen estimator, and 32,000 runs in the case of original Sobol estimator. In both cases, 95 % confidence intervals were generated with 100 bootstrapped replications.

3. Results

3.1. Model performance

In general, validation outputs were in agreement with field observations and empirical data from published sources, suggesting that the simulated individual behaviours and emergent demographic parameters were comparable to those of real populations. In particular, mean extinction rates predicted by the model every 3 months averaged ($\pm$ SD) 8.4 ± 2.6 %, ranging between 6.0–11.7 %, which is in accordance with comparable empirical estimates up to 15.9 % (Fig. 2). Moreover, according to expectations, the model was able to capture the general decrease in extinction rates with increasing patch size, connectivity and habitat quality (Fig. 3 and Supporting information, Section 'Supplementary results', Table S7). As for density, estimates predicted by the model averaged 19.2 ind./ha, ranging between 2 and 159.8 ind./ha, also in accordance with empirical data found in real populations (Fig. 2). Furthermore, as expected, there was an overall increasing trend in density across time and with increasing habitat quality (Fig. 3 and Supporting information, Section 'Supplementary results', Table S7). The average sex-ratio value recorded model outputs (0.48 ± 0.25) was in line with those registered empirically (Fig. 2), tending towards a balance between males and females, although slightly favouring the number of females, as reported in Rosário (2012). Although the estimated mean residence time of 4.1 ± 3.0 months was slightly higher than that recorded in empirical studies (3.5 ± 2.8 months, Fernández-Salvador et al. (2005b)), it was within the range of values recorded in that study (1–12 months) (Fig. 2). It should be noted however that residence times provided in Fernández-Salvador et al. (2005b) may be underestimated, as it was based on capture recapture methods that did not allow for possible heterogeneity in individual recapture probability. Overall, therefore, our model seems to accurately recreate the post-colonization demography of voles within local population.

3.2. Sensitivity analysis and support for main predictions

Bootstrapped estimates of LHS-PRCC between patch attributes and emergent demographic responses showed very low bias (<0.01), indicating a high stability of the estimates. However, although the results were statistically significant in most cases, correlations were generally weak ($<|0.3|$) (Fig. 4).

Our simulations indicated high variability in both B-I and I-E indexes (mean $\pm$ SD [range] of 0.17 ± 0.71 [$-1.00 - 1.00$] and -0.21 ± 0.61 [$-1.00 - 1.00$], respectively), suggesting high variation in both self-recruitment and contribution of local populations to other patches. As predicted, the B-I index correlated negatively with patch size and connectivity shortly after colonization, though, over time, this relation became positive (Fig. 4 and Supporting information, Section 'Supplementary results', Fig. S2), concurrently with the increases also observed in density (Fig. 3). In addition, the B-I index correlated positively with habitat quality across time (Fig. 4 and Supporting information, Section 'Supplementary results', Fig. S2). Also, according to expectations, the model predicted a positive-to-negative shift in the relationships between the I-E index and patch size and connectivity over time (Fig. 4 and Supporting information, Section 'Supplementary results', Fig. S2). Furthermore, the model also supported the prediction that habitat quality negatively affects the I-E index (Fig. 4 and Supporting information, Section 'Supplementary results', Fig. S2).

When considering Sobol's indices as a whole, sensitivity patterns to patch size, quality and connectivity were broadly similar for the two

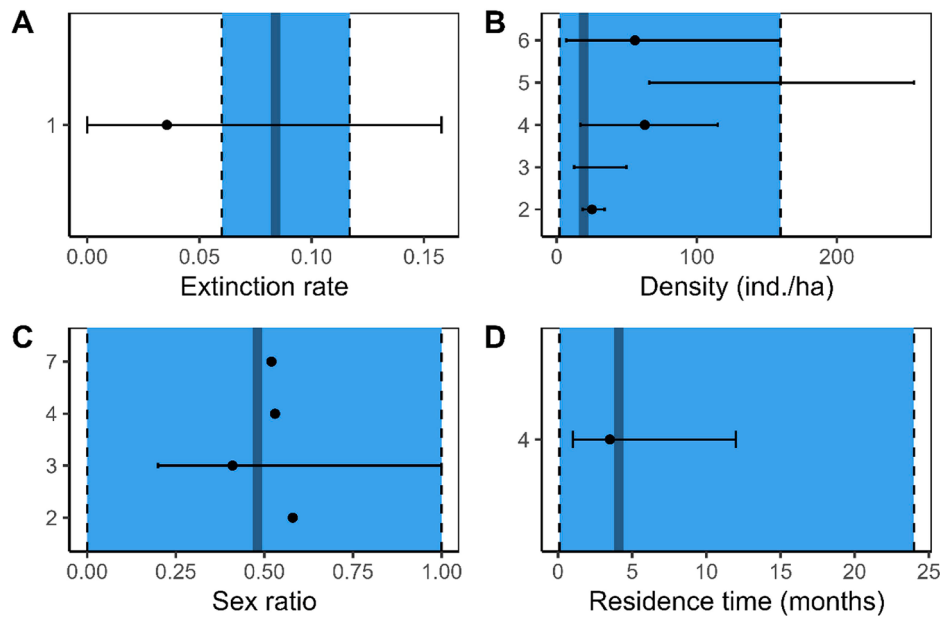


Fig. 2. Comparison of the model's validation outputs with estimates from the empirical literature. Validation output corresponds to the mean (vertical grey line) and standard deviation (range in blue) of each parameter collected every three months of the simulations. Empirical point estimates (black points) and uncertainty (bars) are numbered as: 1 - "Pita et al. (2007)"; 2 - "Sabino-Marques et al. (2018)"; 3 - "Rosário (2012)"; 4 - "Fernández-Salvador et al. (2005b)"; 5 - "Landete-Castillejos et al. (2000)"; 6 - "Peralta et al. (2023)"; 7 - "Proença-Ferreira et al. (2019)".

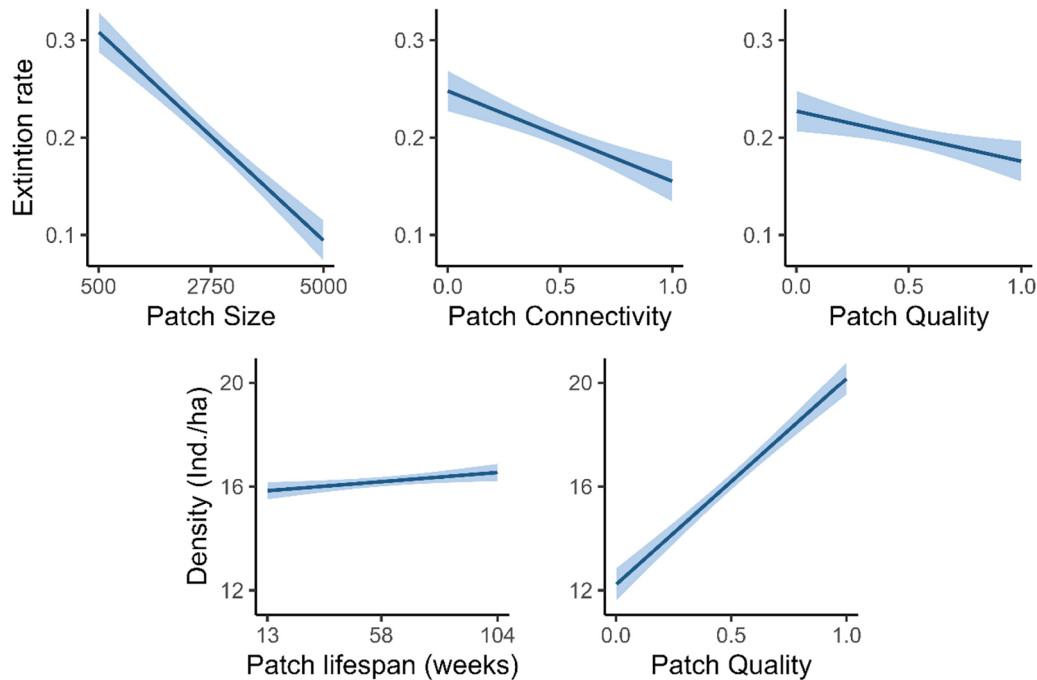


Fig. 3. Linear regressions (lines and 95 % confidence intervals) showing the general trends in validation outputs, matching expectations from general ecological theory. Data used to represent these relationships were derived from the original Sobol estimator simulations (see main text and Supporting information, section 'Supplementary results', Table S7).

focal emergent outputs along patch lifespans (Fig. 5), supporting the prediction on the relevance of single versus interaction effects over time. Specifically, the size of the patch alone was in general the only factor exerting influence by itself (S_i), though this influence decreased over time, becoming negligible for most of the parameters by the end of the simulation. Notably, the total effect of patch size (S_{Ti}), strongly influenced model outputs throughout the whole simulation period, with sensitivity indexes always close to 1. Conversely, the total influence of patch quality and connectivity had negligible impacts shortly after

colonization, though the sensitivity of model outputs to these variables greatly increased along the simulation period. In the case of patch quality, total indices generally began to show sensitivities greater than 0.5 about six months post-colonization, stabilizing after one year at ca. 0.75. In the case of connectivity, total sensitivity indexes generally only exceeded 0.5 around one year and a half after initial colonization, reaching the breakeven point after ca. one year (Fig. 5). When comparing the first-order and total-order indices, both the B-I index and the I-E index were highly sensitive to the interaction among patch

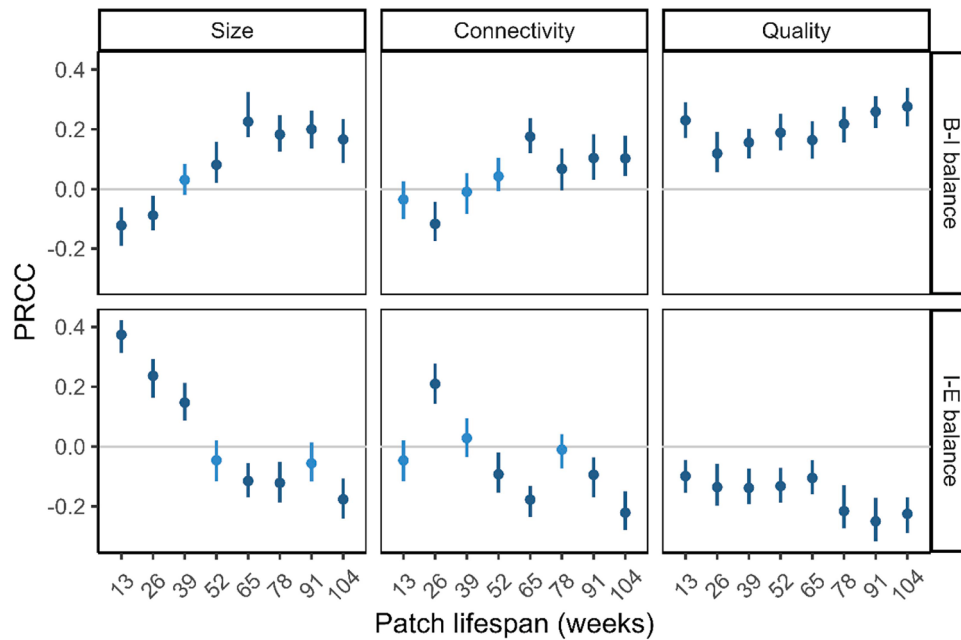


Fig. 4. Partial rank correlation coefficients (PRCC) and 95 % confidence intervals between the focal demographic indices (rows) and habitat properties (columns) over the simulation period. The lighter blue dots represent PRCC values that are not statistically significant. For a full report regarding all emergent outputs of the model (see Supporting information, Section ‘Supplementary results’, Fig. S2).

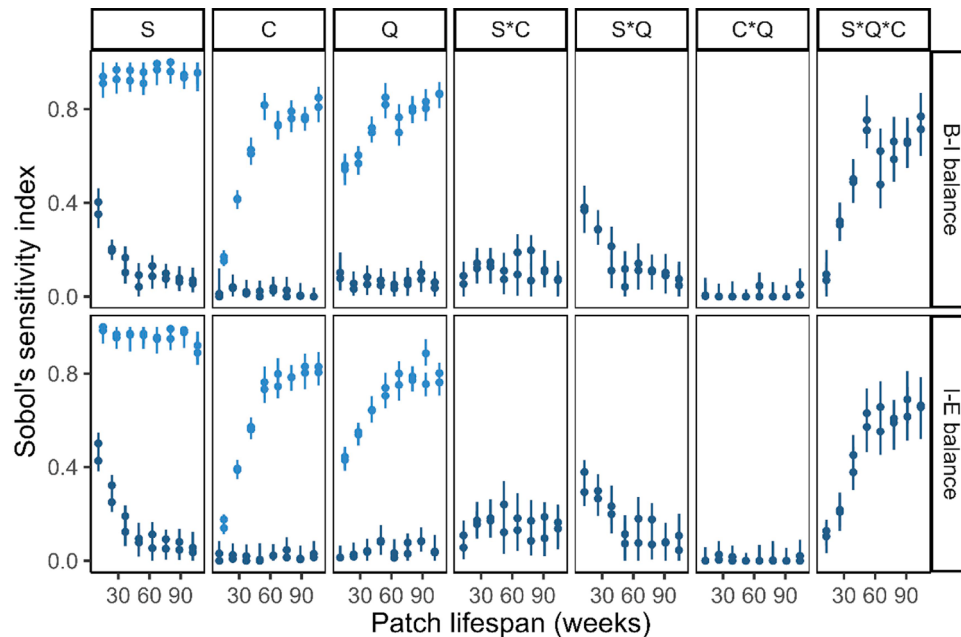


Fig. 5. Sobol's sensitivity indices and 95 % confidence intervals between the focal demographic indices (rows) and local patch attributes (columns) over the simulation period. S – patch size, C – patch connectivity, and Q – habitat quality. The first 3 columns on the left presents the estimates of the Sobol's first-order (S_i – darker blue) and a total-order (S_{Ti} – lighter blue). Columns 4 to 6 presents the estimates of the Sobol's second-order (S_{ij}), and the last column the estimates of the third-order (S_{ijk}).

attributes rather to their main effects (i.e., very different S_i and S_{Ti} values for both parameters). In particular, the interaction among the three input factors (S_{ijk}) was of major relevance for the demographic responses considered. Indeed, despite being largely irrelevant shortly after colonization (< 6 months), the interaction among patch size, quality and connectivity became increasingly important over time, showing a stabilization trend after the first year post-colonization, with respective indices always > 0.4 for both demographic indexes considered (Fig. 5). Second-order interactions (S_{ij}) played a generally minor

role, with the interaction between size and quality showing, in some cases, a moderate importance (often > 0.3 and < 0.4) shortly after colonization, tending to decrease along the simulation period. The interaction between size and connectivity showed a weak influence, with the 95 % CI's of estimated Sobol indices mostly comprising values close to 0. Regarding the interaction between connectivity and quality, Sobol indices consistently presented values close to 0 throughout the simulation for both demographic indexes considered (Fig. 5).

4. Discussion

Our individual-based model inspired by the threatened Cabrera vole occurring in heterogeneous ephemeral patches provided evidence that considerable spatial and temporal variation may emerge in local populations' self-sustainability and contribution to other patches, according to variation in the size, internal quality, connectivity, and lifespan of habitat patches. This corroborated our overreaching hypothesis that patch spatial attributes and time to disturbance affect the emergence of temporary source local populations, with evidence suggesting the presence of strong interaction and synergistic effects among these factors. The idea that patch spatial attributes should not be considered alone and independently of each other when predicting the source-sink status of local populations in spatially and temporally heterogeneous environments (Heinrichs et al., 2019, 2015; Robles and Ciudad, 2012; Wright et al., 2020) is supported by our model. Importantly, the lifetime of habitat patches relative to species generation times played a critical role in post-colonization transition of local populations from sink to source, confirming the prediction that short times to disturbance should preclude the emergence of temporary source local populations (e.g. Fahrig, 1992; Van Teeffelen et al., 2012). Given the challenge of distinguishing between source and sink local populations in real ecological systems, these results are particularly relevant in highlighting that conventional and readily measurable or predictable patch-level characteristics, such as those considered here, may provide a valuable indication of the source-sink potential of local populations in ephemeral patches. While further empirical testing is needed to confirm our findings, they still strengthen the view that different conservation management strategies at local scales may be required according to the source-sink potential of target habitat patches (Furrer and Pasinelli, 2016; Heinrichs et al., 2019).

4.1. Emergence of source local populations of Cabrera voles in ephemeral patches

According to our model, Cabrera vole local populations occurring in large and well-connected high-quality patches may behave as temporary sources at some time after initial colonization. In line with predictions, habitat patch internal quality correlated positively with demographic metrics describing the increase in vole population self-sustainability and potential contribution to other patches throughout time since colonization by a founder breeding pair. However, the strength of these relationships was mostly relevant only after about three generation times (ca. one year) since initial colonization, and only in combination with the positive effects of patch size and connectivity. Prior to this, self-sustainability and contribution strength decreased with increasing patch size and connectivity, with patch size effects being by far the most influential. The change in the direction of these relations over time reflects the gradual filling of physical space by voles in large patches during the first generations following colonization, and, to a lesser extent, the arrival of immigrants before in situ growth fills the patches. Therefore, our results corroborate the idea that the source-sink potential of individual patches might not be accurately inferred from local habitat quality alone, as earlier posited (Pulliam, 1988), and that complex interactions with other sources of patch spatial variability, such as size and connectivity, may determine the emergence of sources (e.g. Nisi et al., 2023; Schumaker et al., 2014). Notably, these complex dynamics unfolded only when local populations in large and well-connected high-quality patches transition from high immigration and low emigration during the low-density phase to low immigration and high emigration as local density increases, which implies patches persisting for over one year (>3 vole generations). This highlights the role of density-regulated processes determining the source-sink status of habitat patches from initial colonization to patch disturbance, with local populations operating below their carrying capacity having much lower chances of becoming source populations (e.g. Heinrichs et al., 2016).

Therefore, based on our results and consistent with other studies, we suggest that variation in local patch attributes should provide a particularly influential context to strengthen source-sink dynamics in real landscapes.

While our model did not consider dispersal mortality of emigrants, the above influence of patch attributes on source-sink status of Cabrera vole local populations over time could potentially suggest that in real landscapes subjected to high habitat turn-over (disturbance frequency at intervals shorter than one year), the occurrence of high-quality, yet small and isolated patches would disproportionately support metapopulation persistence more significantly than their large and well-connected counterparts. Although this remains to be formally tested, such a scenario is expected to weaken the establishment of source-sink dynamics, where metapopulation persistence with high turnover of patches would require low dispersal mortality (e.g. Gundersen et al., 2001; Mestre et al., 2020). Moreover, it's important to note that, even within high-quality habitats, populations within small and poorly connected patches were generally more susceptible to stochastic extinction. This made them less prone to function as potential temporary sources, unlike local populations persisting in large, well-connected patches for over a year since colonization. These results thus support the expectation that habitat stability is important in predicting temporary source local populations in ephemeral patches (Heinrichs et al., 2016). Specifically, in the case of the Cabrera vole, eventual transitions from sink to (temporary) source seem conditional upon patches persisting for over at least one year post-initial colonization, with this broader underlying pattern apparently holding beyond the seasonal fluctuations that may occur in demographic trends within local populations. The consequences of severe synchronous adverse seasonal effects (e.g. drought) on habitat patch-network properties in real landscapes may however warrant particular attention, as these may pose a potential challenge to metapopulations responsive to ongoing climate change, as seems to be the case of the Cabrera vole (Mestre et al., 2015).

4.2. Model strengths and research implications

In an effort to capture the essence of Cabrera voles' local population processes within habitat patches amid a hostile matrix, we developed a stochastic individual-based model for simulating spatially explicit within-patch demography while considering implicit landscape (among patch) processes, informed by extensive empirical data. Despite the simplified nature of our model, the dimensionality of the parameter space evaluated was considerable, allowing to uncover our main predictions without resorting to complex representations of landscape realities. A further significant merit of our approach is that it focused on two simple and intuitive demographic metrics (B-I and I-E indices) as indicators of local self-sustainability and demographic contribution of temporary local populations to other patches. Although simplified, these metrics remain true to the fundamental demographic properties conventionally considered in source-sink research, while their concurrent use avoids placing particular emphasis on any of these properties, as is often the case of single-metric approaches (e.g. Furrer and Pasinelli, 2016; Sample et al., 2019). Also, according to our results, when assessed sequentially at defined time intervals, these metrics may adequately capture sharp temporal shifts in local populations' demographic trends under transient dynamics (Runge et al., 2006). Still, despite the elegance of our modelling approach, one potential criticism, we acknowledge, is that we restricted the lifespan of habitat patches to up to 2 years. While model outputs suggested considerable less variation in demographic change during latter generations relative to earlier ones, it is possible that such patch lifespan threshold may have constrained our ability to distinguish between relatively stable temporary sources and local populations that fluctuate between source and sink. However, given the relatively rapid turnover in Cabrera voles' habitat in intensively used landscapes (e.g. Pita et al., 2007), the establishment of stable sources over long time periods is mostly unlikely, making it crucial to identify

the local patch attributes that most contribute to short-term sink-to-source transition in ephemeral patches, as explored here.

Although our model was effective in predicting the source-sink status of local populations based on patch spatial attributes and time to disturbance, further experimental and empirical testing of these predictions is needed to enhance the accuracy of our findings. In particular the use of fully spatially explicit landscapes and metapopulation would be crucial to infer about the scenarios under which source-sink like dynamics may occur in dynamic environments. While the use of replicated microcosms containing simplified versions of ecological systems (e.g. for small invertebrates like mites and daphnia) may help elucidate our understanding of source-sink dynamics in ephemeral habitats (Benton et al., 2007), such approaches still lack the context-specific details of complex natural systems. Conversely, empirical testing of results from simulation-based source-sink research is typically difficult to operationalize, given the costs often involved in intensive collection of demographic data (Heinrichs et al., 2016). However, by contributing to the conceptual understanding of the dynamics that may characterize post-colonization demographics within ephemeral patches, we believe our simulation results may be useful to guide and target the intensive survey efforts required to empirically assess the potential for source-sink dynamics in metapopulations (for instance, by focusing on systems with greater asymmetries in patch size, internal quality, and connectivity). Still, because the absence of empirical testing should not preclude the use of theoretical predictions on the mechanisms driving the source-sink status of local populations (particularly for species needing urgent conservation actions, as is the case of the Cabrera vole), we suggest that our results may be used to inform conservation management. Therefore, should our model insights be transferable to natural systems, it would highlight the need to prioritise the protection of large (up to 5000m²) and well-connected high-quality patches for relatively long time periods (ideally up to 2 years or more), in order to allow the establishment of local populations with some potential to function as sources, at least during some time before a new local disturbance takes place (e.g. mowing, harvesting, ploughing, burning, inundation, overgrazing, drying up), while other source populations recover, emerge, or are created in the system (e.g. Pita et al., 2007). Ensuring ongoing access to habitat patches that once colonized may function as temporary sources, should therefore enhance the likelihood of metapopulation persistence in spatially and temporally heterogeneous environments.

5. Conclusion

Landscape dynamics involving habitat turnover due to natural or human disturbances is widespread (Van Teeffelen et al., 2012), and metapopulation persistence in resulting networks of ephemeral habitats has been frequently associated to source-sink like dynamics (Reigada et al., 2015). Assessing the source-sink status of local populations is therefore important for metapopulation conservation in ephemeral patches, particularly for weighting different management options and timings under limited funding (Hastings, 2003; Keymer et al., 2000; Pasinelli et al., 2011). Our individual-based model grounded in the exceptionally well-studied biology and ecology of the Cabrera vole in Mediterranean farmland provided important insights on how patch size, internal quality and connectivity may jointly contribute to augment or diminish the likelihood of a local population to become temporary source under different patch disturbance rates. While our hypotheses were not directly formulated for real-world populations, expectations from our model should be well-suited for empirical testing, in order to more properly identify the factors potentially inciting sources-sink dynamics, and direct conservation efforts accordingly (Hastings, 2003; Keymer et al., 2000; Pasinelli et al., 2011).

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CRediT authorship contribution statement

Tiago Crispim-Mendes: Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Deon Roos:** Writing – review & editing. **Clara Mendes Ferreira:** Writing – review & editing. **Joana Paupério:** Writing – review & editing. **João Paulo Silva:** Writing – review & editing. **Sérgio Godinho:** Writing – review & editing. **Paulo Célio Alves:** Writing – review & editing. **António Mira:** Writing – review & editing. **Pedro Beja:** Writing – review & editing, Methodology, Conceptualization. **Xavier Lambin:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Ricardo Pita:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Tiago Crispim-Mendes reports financial support was provided by Portuguese Foundation for Science and Technology. Ricardo Pita reports financial support was provided by Portuguese Foundation for Science and Technology. Sergio Godinho reports financial support was provided by Portuguese Foundation for Science and Technology. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data will be made available in the Supporting Information

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2024.110839](https://doi.org/10.1016/j.ecolmodel.2024.110839).

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