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***steps*: software for spatially- and temporally- explicit population simulations**

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Summary

1. Species population dynamics are driven by spatial and temporal changes in the environment, anthropogenic activities, and conservation management actions. Understanding how populations will change in response to these drivers is fundamental to a wide range of ecological applications, but there are few open-source software options accessible to researchers and managers that allow them to predict these changes in a flexible and transparent way.

2. We introduce an open-source, multi-platform R package, *steps*, that models spatial changes in species populations as a function of drivers of distribution and abundance, such as climate, disturbance, landscape dynamics, and species ecological and physiological requirements.

3. To illustrate the functionality of *steps*, we model the population dynamics of the greater glider (*Petauroides volans*), an arboreal Australian mammal. We demonstrate how *steps* can be used to simulate population responses of the glider to forest dynamics and management with the types of data commonly used in ecological analyses.

4. steps expands on the features found in existing software packages, can easily incorporate a range of spatial layers (e.g., habitat suitability, vegetation dynamics and disturbances), facilitates integrated and transparent analyses within a single platform, and produces interpretable outputs of changes in species' populations through space and time. Further, *steps* offers both ready-to-use, built-in functionality, as well as the ability for advanced users to define their own modules for custom analyses. Thus, we anticipate that *steps* will be of significant value to environment and wildlife managers and researchers from a broad range of disciplines.

Keywords: demography, ecological modelling, habitat, metapopulation, matrix models, population dynamics, range shift, SDM

Introduction

The need for spatial and temporal predictions of species' population dynamics in response to environmental change and management actions has long been recognised (Akcakaya et al., 2004; Keith et al., 2008), and population models remain central to ecological management and research (Thuiller et al., 2013). Researchers and conservation managers need to be able to model the cumulative and synergistic effects of multiple drivers of population dynamics, including the amount, quality, and configuration of habitat (e.g. effects of climate and land-use change), stochastic disturbances and catastrophes (e.g. fire), and spatially-varying influences on survival and fecundity (e.g. disease, physiological constraints, predation).

Two well-established modelling approaches used to answer these questions are population viability analysis (PVA) and correlative species distribution modelling (SDM). PVA requires knowledge of species' population dynamics and estimates of vital rates, such as survival and fecundity, to simulate population trajectories and quantify the likelihood of population persistence over a defined time period (Boyce, 1992). Correlative SDM is a statistical modelling approach used to predict species occurrence across a landscape using relevant spatial predictors and has been widely used to predict potential impacts of environmental change and management interventions on biodiversity (Guisan et al., 2013). Correlative SDM enables users to make spatial and temporal predictions of species occurrence when these are the only data available. However, these models do not explicitly account for dynamic population processes, such as dispersal, spatial and temporal variation in vital rates, and density-dependence, and so may not provide reliable predictions of species persistence (Fordham et al., 2012).

To address some of these limitations, spatially-explicit population models (SEPM) have been developed, which combine spatially-explicit data with the population dynamics processes in PVA (Fordham et al., 2013). Typically, SEPM start with spatial information on the availability and quality of habitat patches through time – often derived from correlative SDM. This habitat suitability is combined with information about initial population sizes, vital rates, and dispersal capacity, to predict future population abundances via stochastic simulation (Fig. 1 and Akçakaya et al. 2004; Keith et al., 2008; Beeton et al., 2015).

Despite the potential of SEPM approaches to provide spatially- and temporally-explicit predictions of population abundances, they remain relatively rare compared to correlative SDM (Briscoe et al., 2019). A key barrier to more widespread use is the availability and accessibility of population modelling software. As highlighted by Lurgi et al. (2015), common shortcomings of currently-available population modelling software include limited flexibility for customisation, lack of transparency and reproducibility, restrictions to specific computer operating systems, and advanced computational skills required of users. There are several software options that are open-source and multi-platform, however, these tend to be either highly customisable, but with complex set-up and coding requirements (e.g., *spaDES*), or more straightforward, but with limited modularity and documentation to assist with customisation (e.g., *demoniche* - Nenzén et al., 2012). Other freely available software with extensive built-in functionality may only run on single operating systems and have source code that is not available for users to scrutinise or customise (e.g. *RangeShifter* - Bocedi et al., 2014). One of the most recognised software packages for SEPM is *RAMAS Metapop* (Akcakaya, 1999), which has an intuitive interface and is well supported and tested, but has a license fee, only runs on Windows operating systems, and is not open-source. This prevents users from adding or integrating new modules that capture ecological or population processes that are not already integrated in the software. These limitations prevent more widespread adoption of comprehensive ecological models and inhibit synthesis studies that draw generalisations from the outcomes of a range of case studies and simulations.

We present *steps* version 1.0.0, an *R* package that combines functionality from existing spatial population simulation software with high transparency, and a modular design that allows for future extensions by other researchers. Crucially, our software is open-source - written in the language of the widely used statistical software *R* (R Core Team, 2019) - and provides a zero-cost option for managers, consultants, citizen-scientists, and others across many different sectors.

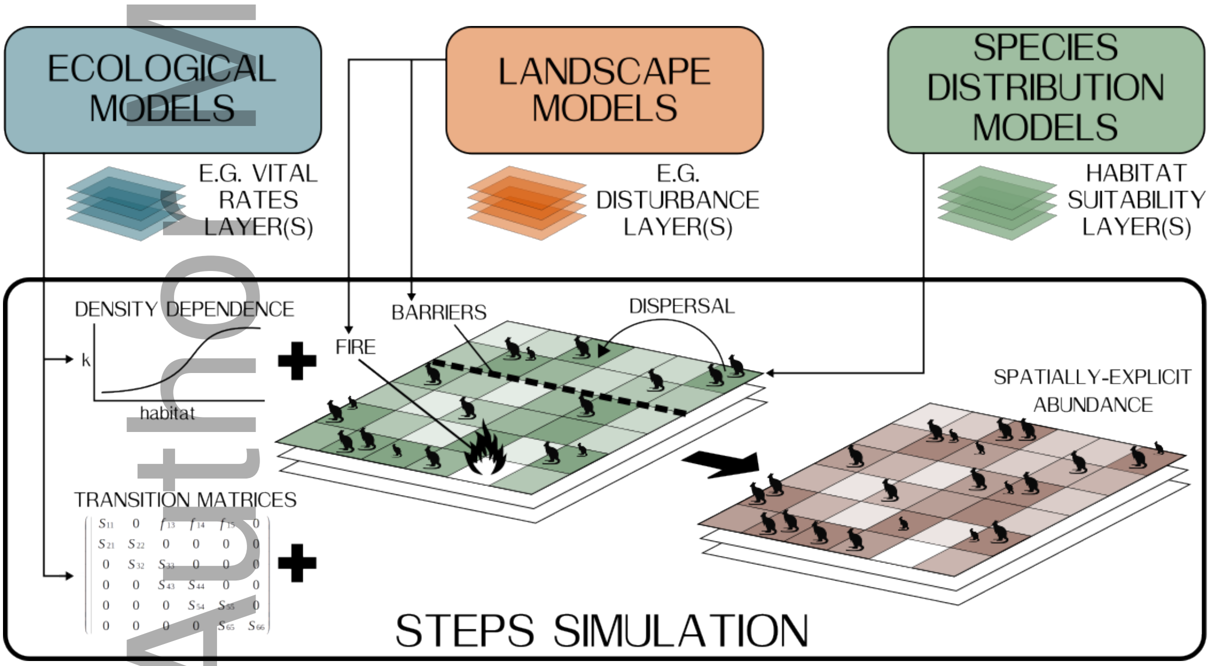

Figure 1: *steps* is run on a grid-based architecture, which enables the easy integration of spatial products (grids) from other modelling software, including climate, landscape, physiological and disturbance information.

Overview of software

While *steps* can be used to perform non-spatial PVA using information on initial population size and a population growth function, its key aim is to enable spatio-temporal predictions of species populations across a landscape. *steps* uses a regular grid to spatially represent a landscape and define carrying capacities, initial abundances, and other miscellaneous spatial information that can be used to define and modify population or landscape features (e.g. translocations or habitat disturbances). Population dynamics within suitable habitat cells are then simulated based on an age- or stage-structured transition matrix, with populations connected via dispersal (Fig. 1).

Because *steps* uses a regular grid to represent populations, it is straightforward to integrate different ecological models and types of data representing landscapes, habitats and populations (Fig. 1). Examples include defining habitat patches and/or carrying capacities using static or temporally-variable spatial outputs from open-source software for landscape change (e.g. *LANDIS* - Mladenoff, 2004) or species distribution models (e.g. *dismo* – Hijmans et al., 2015); incorporating grids of spatially- and temporally-explicit vital rates (e.g. biophysical models such as *NicheMapR* - Kearney & Porter, 2019); and evaluating the relative benefits to species' populations arising from spatial prioritisations of conservation actions (e.g. protected area designation or conservation management) proposed using packages such as *Zonation* (Moilanen et al., 2009).

steps has been developed to run through the statistical software *R* on any operating system and can easily operate in enhanced computational environments (i.e. high-performance server clusters). *steps* architecture is modular and object-oriented (Fig. 2) to maximise flexibility and be computationally-efficient (Appendix B).

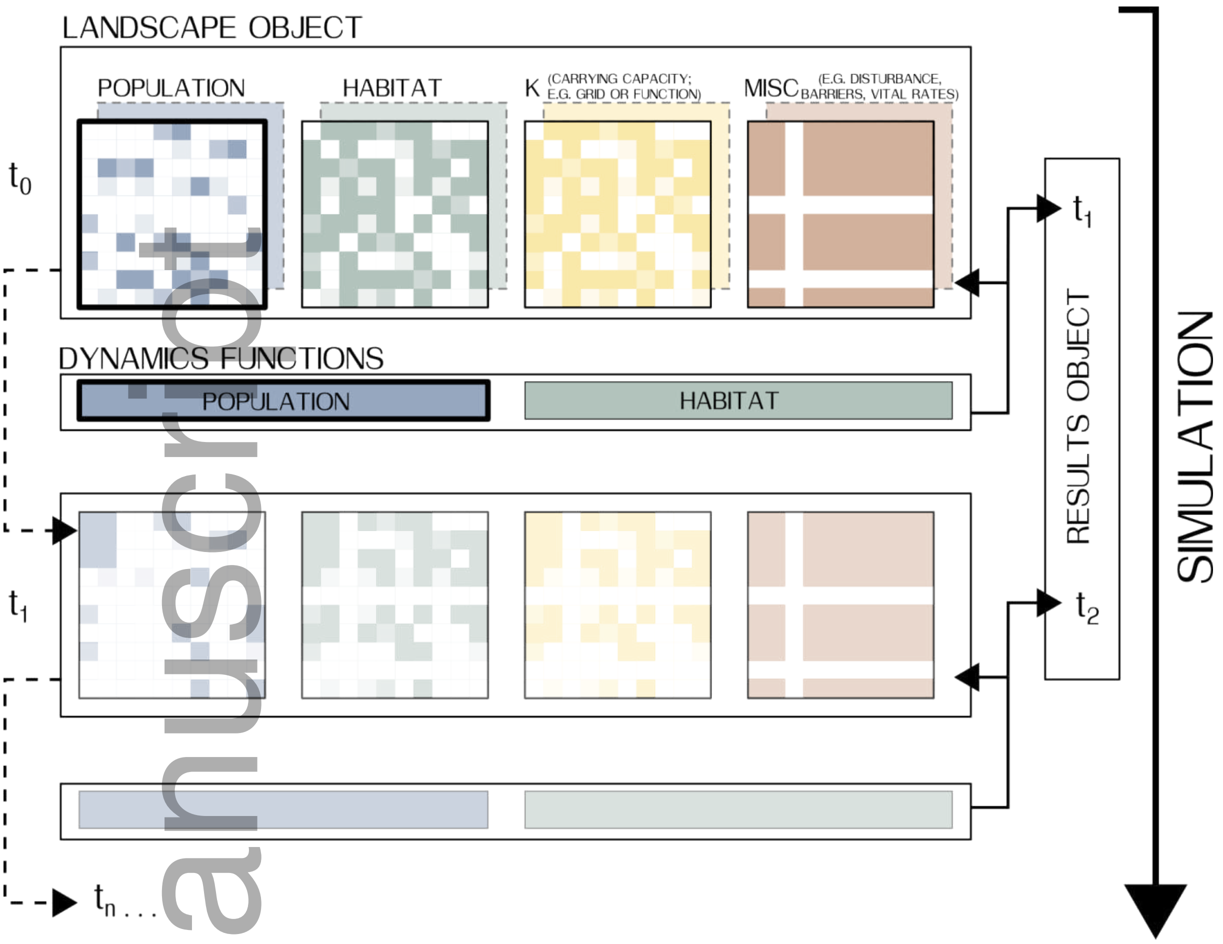

Figure 2: Landscape objects and dynamics functions are passed to a simulation. During the simulation, dynamics are applied to landscape objects at each time step/iteration (t_n) and stored in a results object (solid arrows). The landscape object is modified and reused at each iteration (dashed arrows). Only initial populations and a population growth function (bold boxes) are required to run a simulation - this is equivalent to a non-spatial population viability analysis.

Software functionality

steps includes pre-defined functions to control changes in population growth, dispersal, density dependence, and modifications to populations and habitats (Fig. 3). We have included three types of dispersal function: a computationally-efficient diffusion kernel approach using a Fast Fourier Transform, a more flexible diffusion kernel approach in which dispersal can be constrained by habitat suitability or carrying capacity, and a cellular automata dispersal simulation that considers individual-based movements and accounts for landscape permeability. Both competition and ceiling density dependence functions are included to modify vital rates (e.g. Keith et al., 2008) and to cap population sizes (e.g. Zurell et al., 2012), respectively. Direct changes to populations based on management interventions, such as translocations, reintroductions, fertility control, or culling, can be simulated by calling functions to add or subtract cell populations at specified timesteps. Several plotting options are available, including the ability to plot spatial changes in populations over time as animations.

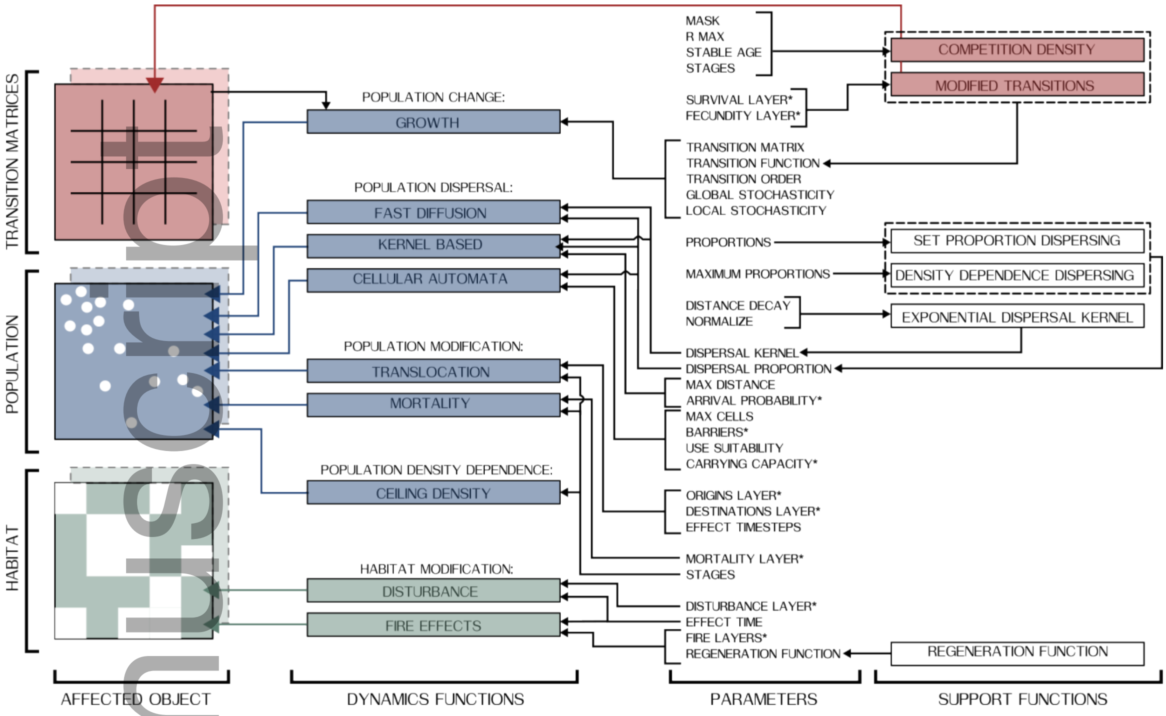

Figure 3: Functionality of *steps*. Boxes in the “dynamics” and “support” categories indicate named inbuilt functions whilst boxes in the “affected object” category indicate landscape objects that are modified by functions during a simulation. Colours and coloured arrows indicate which functions operate on which objects. Black arrows represent information flow (i.e. objects/parameters supplied to functions). Parameters that require spatially-explicit inputs (i.e. grids) are marked with asterisks.

Users are not limited to performing simulations using pre-defined functions - the software accepts any custom function that can be implemented in *R* and we include a tutorial vignette in the software to assist users with creating their own functions. This balance of internal functions that cover many typical operations used in SEPM, and the flexibility to include other operations, offers unlimited potential for users to model and test unique scenarios.

Example

Here we demonstrate the functionality of our software by specifying a greater glider (*Petauroides volans*) SEPM within core habitat in South-Eastern Australia. Greater gliders are folivorous, arboreal mammals that rely on old growth forests for shelter and foraging. We used *steps* to simulate population trajectories over 50 years, accounting for key threats including forest fires. We stress that this example application is provided to demonstrate how to specify a SEPM using *steps*, and not to provide realistic predictions about the viability of the species under planned or proposed management.

Our model landscape is a 250,000 hectare grid with a resolution of 500m x 500m (10,000 total cells). We predicted habitat suitability in each timestep using a correlative species distribution model fitted to occurrence data and dynamic climate and vegetation layers (Appendix A). We set initial population sizes by randomly distributing approximately 4,000 gliders across suitable habitat (likelihood of occurrence >= 0.5) in the landscape. Initial populations were comprised of three life-stages - newborn (~29%), juvenile (~14%), and adult (~57%) - roughly based on stable age distributions calculated from an initial age-based transition matrix (Table 1).

Table 1: A population transition matrix (Lefkovitch matrix) representing post-breeding survival and fecundity values for female greater gliders. The first row indicates the expected number of newborn female gliders per timestep (one year), per individual in each life stage that produce them, multiplied by their respective survival. The second and third rows indicate the expected transition probabilities for the three life stages. The juvenile and newborn life stages each span a year, so there is no probability of an individual remaining in those life stages between timesteps.

	Newborn	Juvenile	Adult
Newborn	0.000	0.425	0.425
Juvenile	0.500	0.000	0.000
Adult	0.000	0.850	0.850

We set up and ran the model using three functions: **`landscape()`**, **`population_dynamics()`**, and **`simulation()`**. We first use **`landscape()`** to create an initial landscape object. This is composed of our initial population raster stack, a habitat suitability raster stack obtained from a species distribution model (Appendix A), and a carrying capacity object - in this case a user-defined logistic `k_function` that will create a raster of maximum population sizes at each timestep based on the corresponding habitat suitability raster. We also include rasters for "fire", "development", and "predation", which are used by the population and habitat dynamics functions to modify population size, carrying capacity, and population parameters, such as survival. A link to code and data used to create our inputs is provided in the “Data availability” section.

```
# carrying capacity as a logistic function of suitability
k_function <- function(landscape, timestep) {
  suit <- landscape$suitability[[timestep]]
  25 / (1 + exp(-(suit - 0.5) / 0.05))
}

glider_landscape <- landscape(population = glider_pop_500,
                              suitability = glider_hab_suit_500,
                              carrying_capacity = k_function,
                              "fire" = glider_hab_fire_500,
                              "development" = glider_hab_clear_500,
                              "predation" = glider_owl_predation_500)
```

We use **`population_dynamics()`** to specify the functions to be executed on the landscape object at each timestep. We indicate that the population will grow according to a baseline transition matrix (Table 1), but with environmental stochasticity in each of the values. The transition matrices for each cell will be modified at each timestep by density-dependent competition between juveniles and adults, and by fires (affecting only survival).

We use cellular-automata dispersal and specify the maximum number of cells (five) across which individuals (juveniles only) move in each timestep to approximate a mean dispersal distance of one kilometre. We also use a function to set the proportion of individuals that disperse based on how close the population of a cell is to its carrying capacity. To simulate predation effects from owls, we use ‘predation’ rasters that define cells where predation reduces the population of juveniles by 50%.

```
glider_pop_dynamics_ls <- population_dynamics(
  change = growth(transition_matrix = glider_trans_mat,
                  global_stochasticity = 0.005,
                  transition_function = list(competition_density(stages = c(2, 3)),
                                             modified_transition(survival_layer = "fire"))),
  dispersal = cellular_automata_dispersal(max_cells = c(0, 5, 0),
                                          dispersal_proportion = density_dependence_dispersing()),
  modification = mortality("predation", stages = 2),
  density_dependence = NULL
)
```

Lastly, we use **`simulation()`** to run population dynamics simulations across the landscape for the specified number of timesteps and replications, and return the results. We provide our landscape and population dynamics objects and specify ten replicates of fifty timesteps for the simulation.

```
glider_baseline <- simulation(landscape = glider_landscape,
                              population_dynamics = glider_pop_dynamics_ls,
                              habitat_dynamics = NULL,
                              timesteps = 50,
                              replicates = 10)
```

We illustrate two of the available options for plotting simulation results: trajectories of the total population of each life stage across the landscape (Fig. 4) and spatial grids (Fig. 5). For the greater glider, both plots indicate a sharp decline, due to a large fire occurring in year nine, followed by population stabilisation.

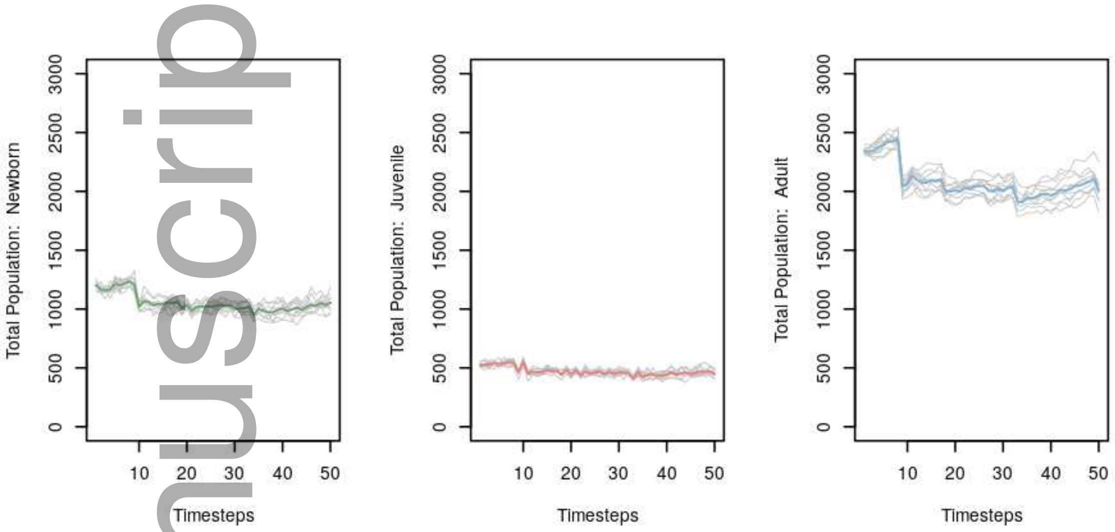

Figure 4: Population trajectories over 50 years for each life stage. Grey lines represent simulation replicates (ten total) whilst coloured lines are mean values.

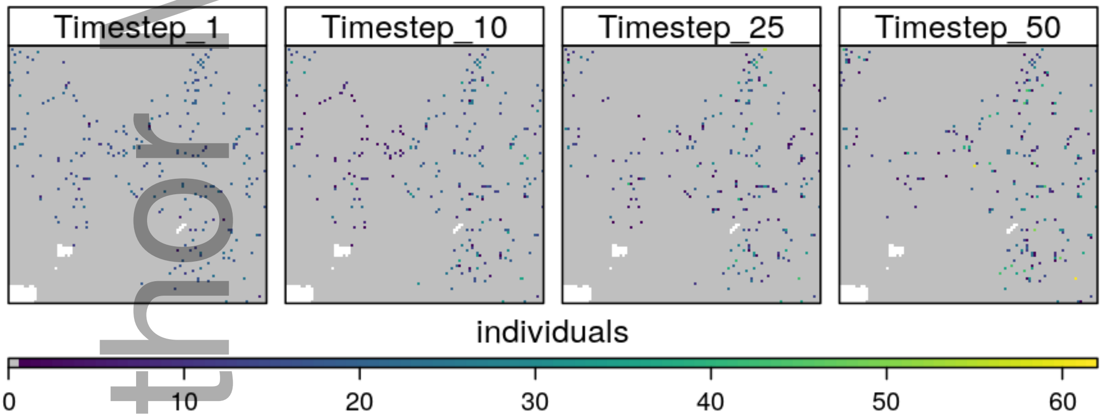

Figure 5: Spatial representations of total population sizes in each 25ha grid cell for years 1, 10, 25 and 50 of a single simulation replicate. Grey areas have zero population and white areas indicate cells with missing values (e.g. water bodies).

By adding functions or changing input data and parameters, we can test management scenarios for the greater glider. As fire and logging were already incorporated into predicted habitat suitability, we tested the effect of clearing approximately 43,000ha in the landscape for urban development to assess population responses. This was done by adding a habitat dynamic function that applied yearly disturbance layers to the habitat suitability rasters. We provided a raster stack representing additive habitat clearing in each year containing zeros (cleared), and ones (no modification), which was multiplied by the habitat suitability raster at each timestep.

```
glider_habmod <- simulation(landscape = glider_landscape,
                   population_dynamics = glider_pop_dynamics_ls,
                   habitat_dynamics = list(disturbance(disturbance_layers = "disturbance")),
                   timesteps = 50,
                   replicates = 10)
```

The simulation resulted in a corresponding change in the population trajectories of the species. Whilst the population once remained relatively stable after the fire (Fig. 6a), it now continued to decrease due to habitat modification (Fig. 6b).

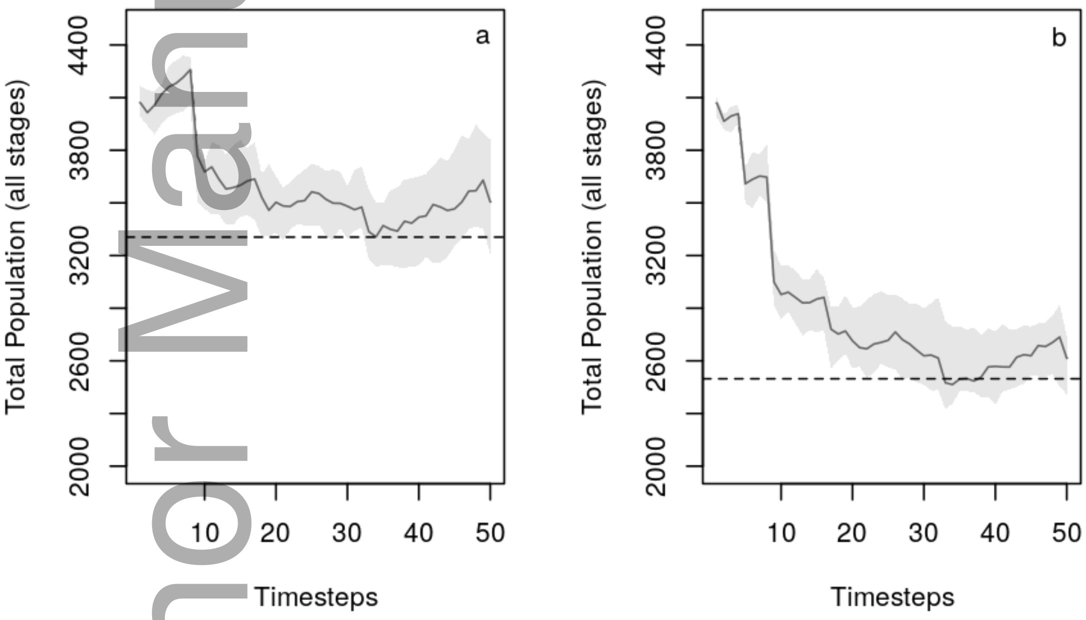

Figure 6: Total population trajectory over the next 50 years with (a) no habitat clearing for urban development and (b) habitat clearing for urban development across the landscape. The grey area represents variability (95% interval) amongst all simulation replicates (ten total) whilst the heavy black line represents mean values. The dotted line is the mean of the minimum population estimates across all replicates.

Simulation results can also be summarised across different management or environmental change scenarios, or under varying model assumptions, using ‘expected minimum abundance’ (EMA) plots (McCarthy & Thompson 2001). EMA is the mean of the minimum total population size across all simulations. These plots allow the user to assess the sensitivity of predictions to model assumptions, or to management or environmental change scenarios. In addition to simulating disturbance, we tested each scenario with two different values of environmental stochasticity (expressed as the standard deviation on survival and fecundity values) - a low value of 0.005 and a ten-fold higher value of 0.05. Fig. 7 shows a comparison of all four simulations.

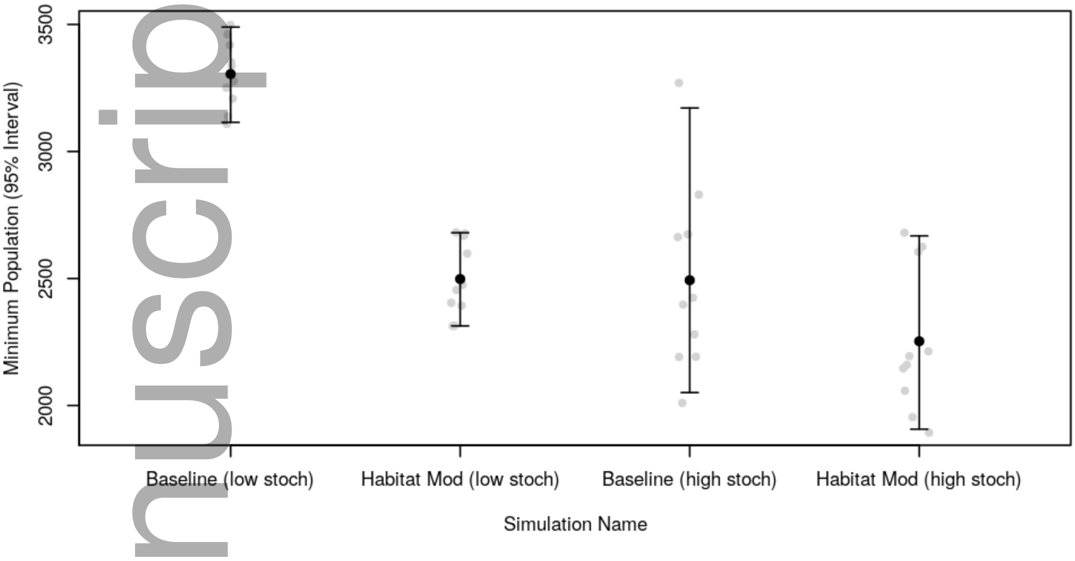

Figure 7: Expected minimum abundance (EMA) for different simulated scenarios, with and without habitat modification, and at both high and low levels of environmental stochasticity. The black dots represent expected minimum abundance across all simulation replicates (each shown as a grey dot).

Discussion

We have developed open-source, flexible, and interoperable software that will enable widespread and reproducible spatially-explicit simulations of species population dynamics. *steps* offers many features currently available in commercially-licensed or platform-specific population simulators – including dispersal, density-dependence, growth, and habitat dynamics – as well as the ability to explicitly incorporate threats and management actions that can vary through space and time.

The grid-based approach adopted in *steps* differs from existing software such as *RAMAS Metapop*, which represent landscapes using discrete habitat patches, which may differ in size and shape. This has several advantages, for example, switching from small, isolated, defined patches to more continuous landscapes is problematic when attempting to sensibly model dispersal using patch-based approaches. Patch-based models also result in a loss of spatial information and, given the increasing availability and quality of grid-based data, this may reduce model utility and flexibility. However, grid-based model performance is dependent on the user selecting a suitable cell size for analyses (see below). If motivated, users could simulate patch-based environments by aggregating cell populations and setting all cells between patch-group cells to missing values. This may increase computational efficiency since *steps* internally ignores all missing values.

Given that *steps* uses a regular grid to spatially organise a landscape, it is important for the user to carefully consider the size of cells. For example, species attributes, such as home range size and activity patterns, should influence the choice of grid cell resolution. In our example, we chose a grid cell resolution of 500 m by 500 m (25ha). We could have chosen a cell size that is closer to the 1.5ha mean home range of greater gliders, as they tend to forage close to shelter; however, this would only allow a maximum of two animals in each grid cell. These low carrying capacities make the populations in each cell more sensitive to demographic stochasticity (although this can be turned off globally), which may not be ecologically realistic in some circumstances. Where users are unsure about the appropriate grid cell size to use, we recommend considering a cell size that sets the maximum carrying capacity to more than a few individuals in highly suitable cells. Users may need to experiment by toggling demographic stochasticity on and off to find a workable, and ecologically reasonable, cell size.

Although we chose to simulate a management action that affected the amount and spatial arrangement of available habitat, it is also possible to test impacts on population dynamics by simulating processes that alter survival and/or fecundity (e.g. disease, heatwaves, drought), including how these vary spatially and temporally. Our example analysed a species of conservation concern, however, the modelling approach could equally be applied to management of overabundant or pest species. *steps* provides a simple starting point, but a remarkable amount of flexibility, enabling users to integrate models, data, and functions to produce robust and transparent predictions about population change across landscapes.

Future work

We intend to develop an online repository for custom *steps* modules and advanced tutorials, allowing users to share custom-written functions (e.g. management interventions or data extracting utilities) for use with *steps*. Most importantly, a publicly-accessible repository will further support our main motivation for developing the software - transparency, flexibility, and reproducibility.

Acknowledgements

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Authors' contributions

B.A.W., S.N.C.W. and N.J.B. conceptualised the modular SEPM freeware. N.G. devised the software architecture. S.N.C.W. and B.A.W. developed early prototypes of the software. C.V., S.N.C.W. and N.G. led the advanced software development and testing. C.V. primarily wrote, documented and published the software and led the writing of the manuscript. N.J.B. and B.A.W. provided data for the example case study. N.J.B, P.E.L. and R.T. advised on the functionality of the software and its applicability to management. All authors performed extended testing of the software and contributed to the manuscript.

Software accessibility

The current development version of *steps* is hosted on Github at: https://github.com/steps-dev/steps. The latest stable version of *steps* can be installed from the comprehensive R archive network (CRAN), within R, or directly at: https://cran.r-project.org/web/packages/steps.

Data availability

VISINTIN, CASEY; BRISCOE, NATALIE; Woolley, Skipton; LENTINI, PIA; Tingley, Reid; WINTLE, BRENDAN; et al. (2020): Spatially- and temporally-explicit population simulator (steps) R package - supporting data. University of Melbourne. Dataset. https://melbourne.figshare.com/articles/Spatially-_and_temporally-explicit_population_simulator_steps_R_package_-_supporting_data/11608392

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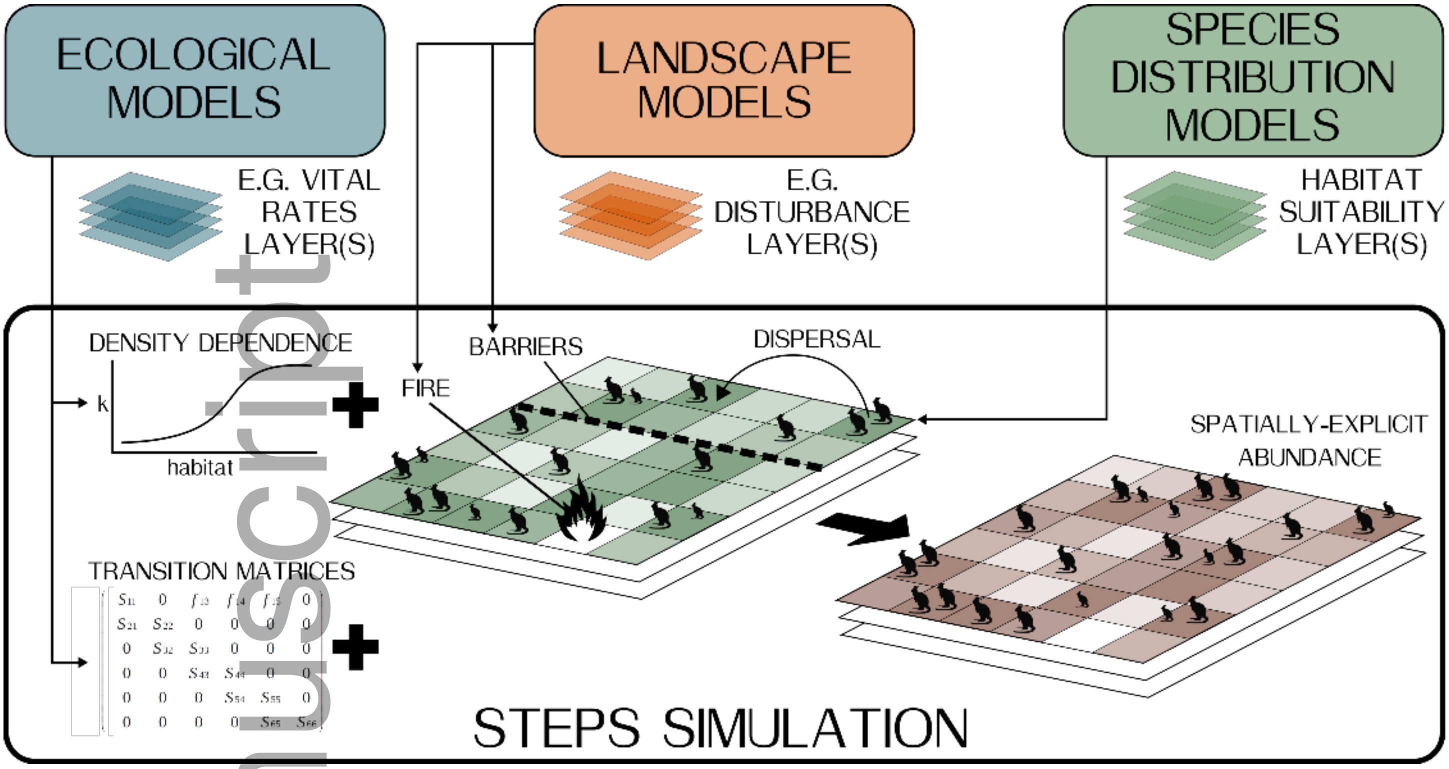

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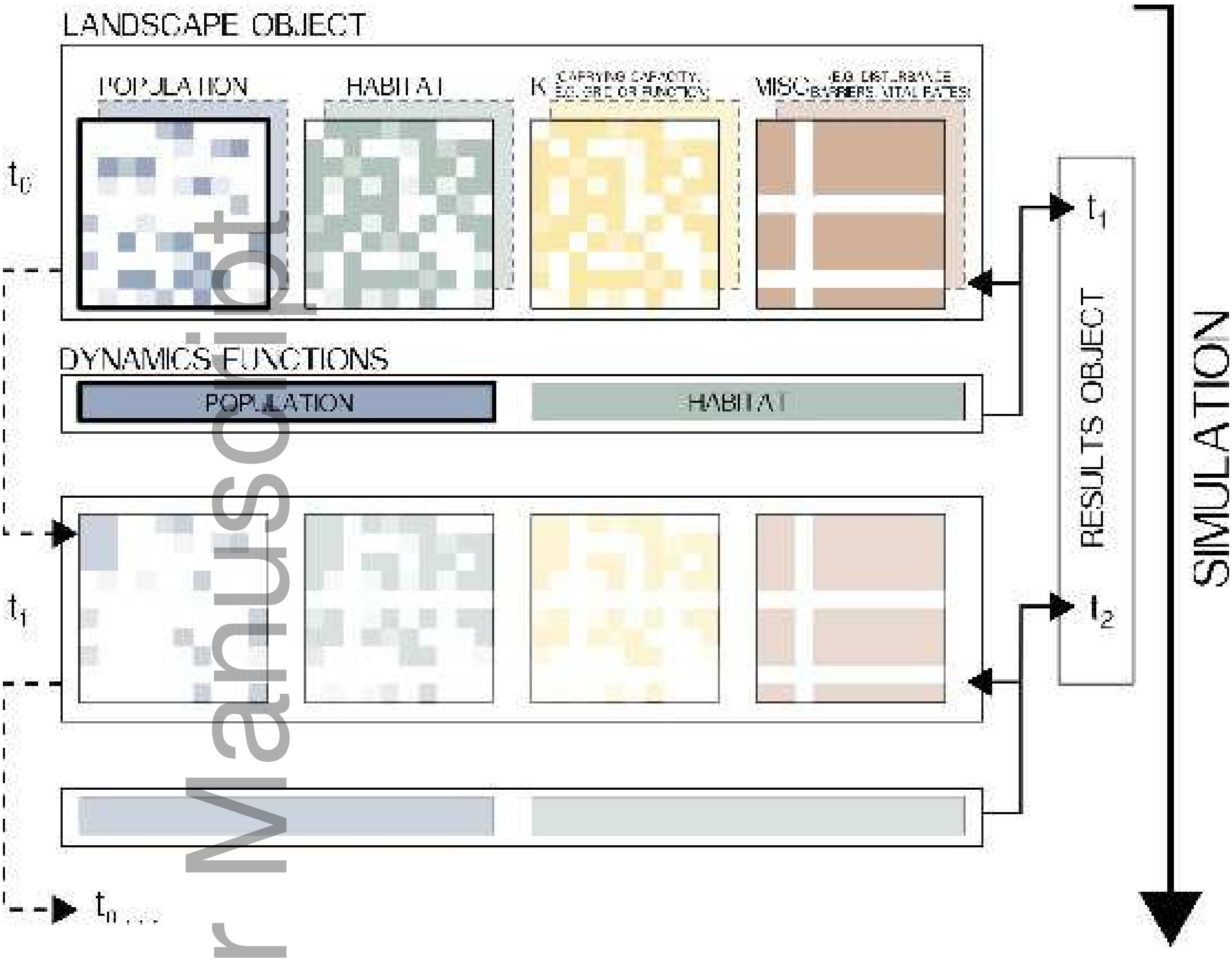

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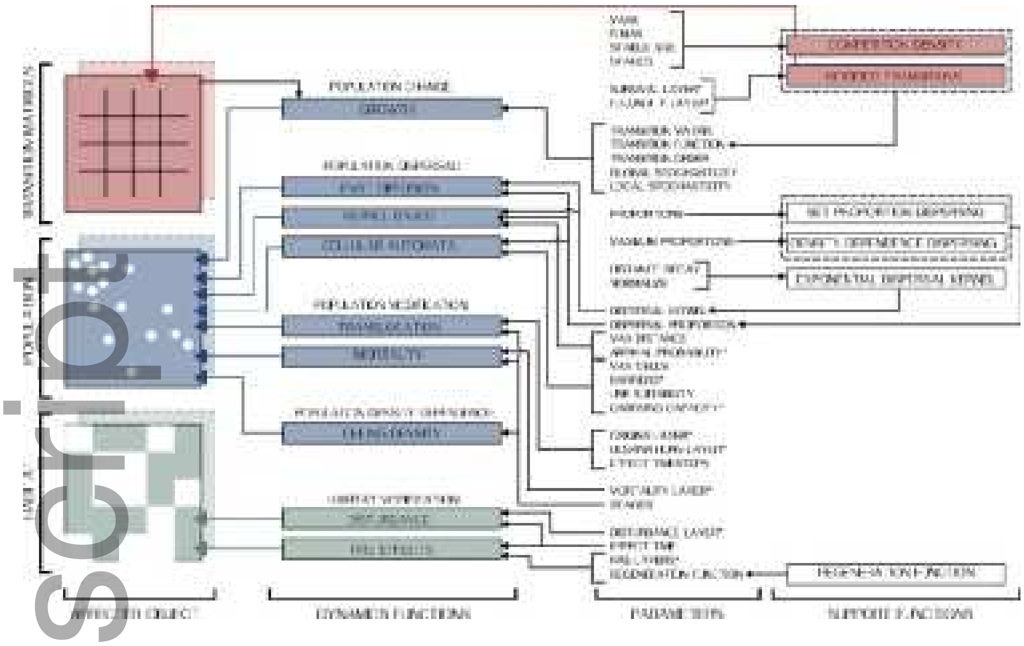

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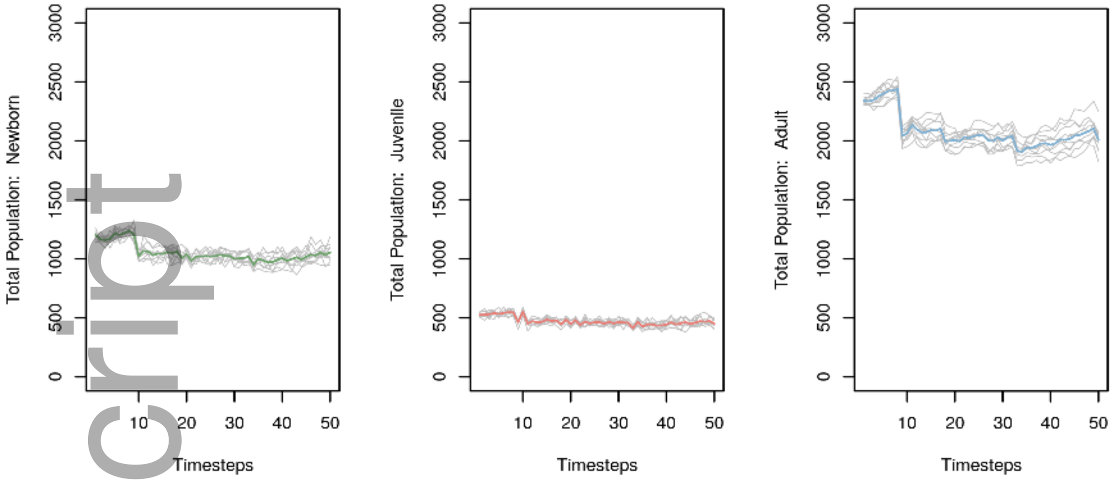

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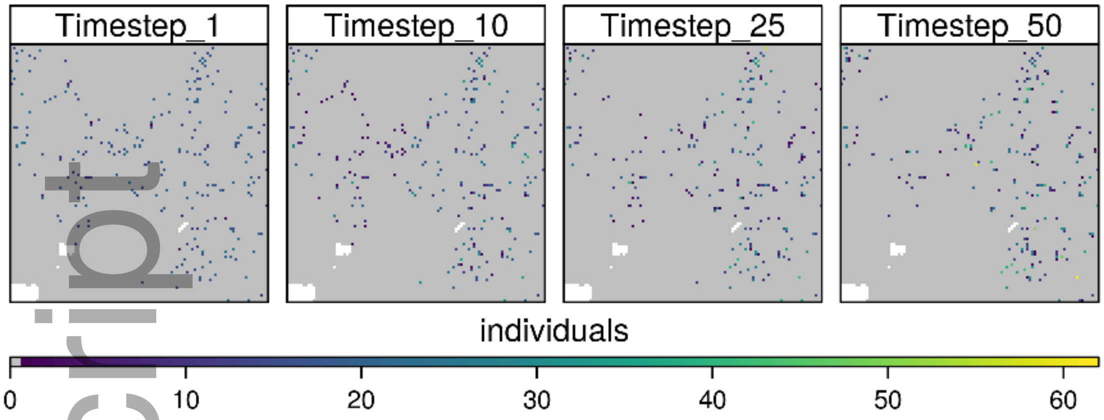

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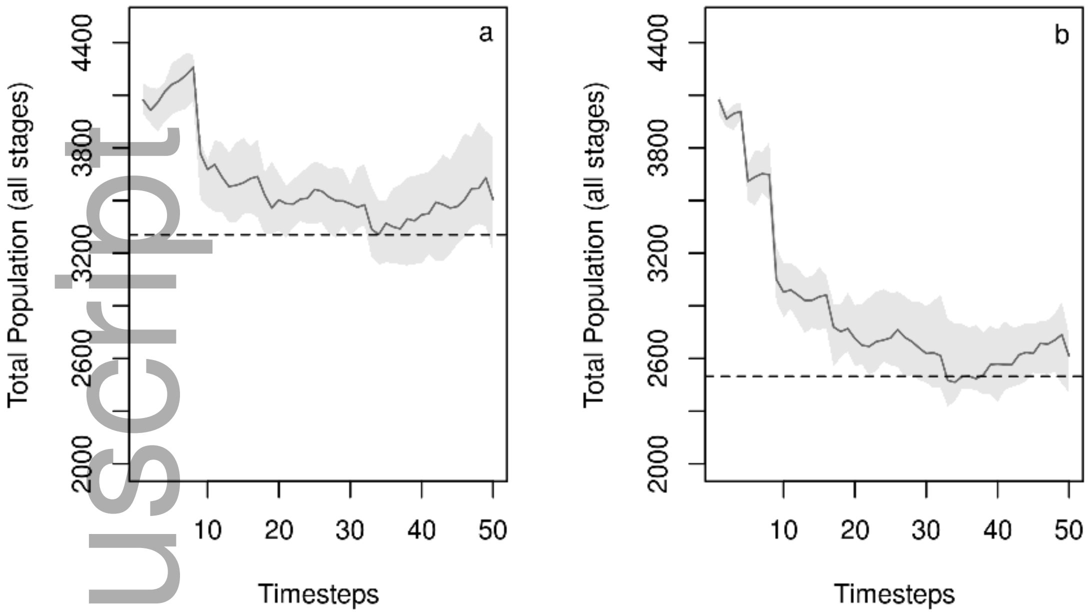

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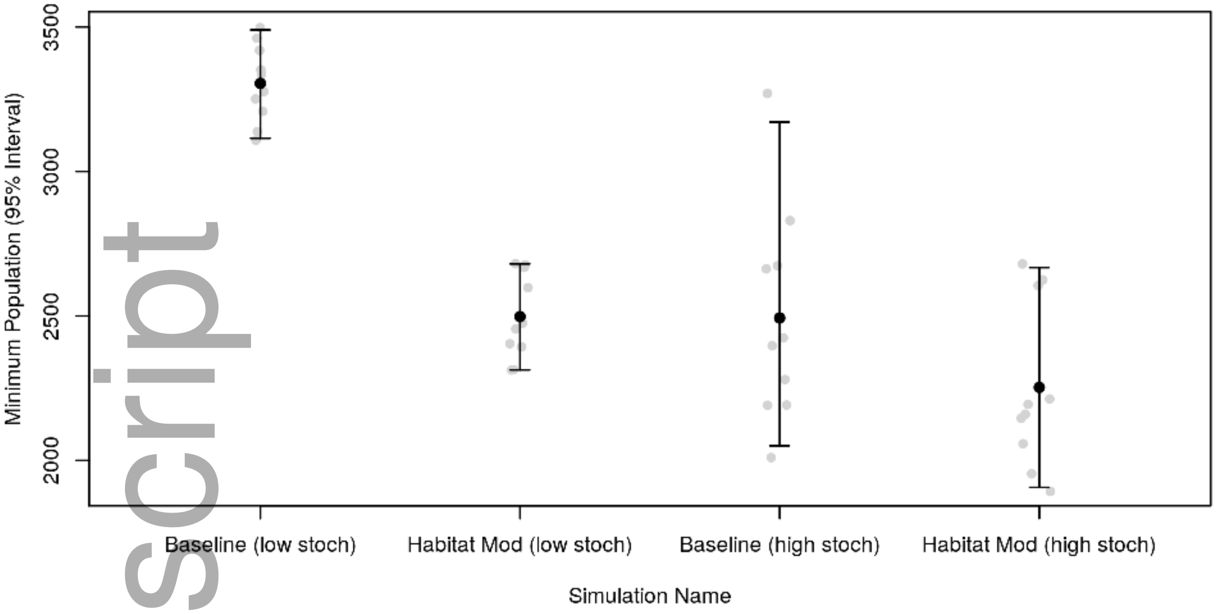

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