demoniche – an R-package for simulating spatially-explicit population dynamics

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demoniche is a freely available R-package to simulate stochastic population dynamics in subpopulations of a species. The demographic model projects population sizes with various transition matrices that represent demographic impacts on species growth. The demoniche model offers flexible options for stochasticity, density dependence and dispersal. Demographic projections are linked to a time-series of geographically distributed niche values that affect the species growth. With the demoniche package it is possible to investigate future population sizes, extinction probabilities and range shift of a species under the influence of scenarios of environmental and human impacts.

Demographic models use transition matrices and the initial population size and stage distribution of a species to study its population dynamics (Caswell 2001, Morris and Doak 2002). Demographic models can also be used to investigate effects of environmental and human changes on a species' growth and persistence, by employing transition matrices that represent different scenarios of population growth, or by modifying the matrix values according to environmental conditions. Models can be made more realistic by simulating different sub-populations distributed in an area, and by including migration between them.

Population models are the basis for Population Viability Assessments that are used for UICN Red listing decisions and wildlife conservation management (Sjögren Gulve and Ebenhard 2000, Akçakaya et al. 2002, Salguero-Gómez and De Kroon 2010). Keith et al. (2008) and Hunter et al. (2011) are two examples of how demographic and environmental modelling can be linked to improve conservation management actions. Since demographic modelling needs detailed species knowledge, we can assess uncertainty in results to see where to focus data-collection.

Various free-standing demographic modelling software exist with unmodifiable source codes: Vortex (Lacy et al. 1993), ULM (Legendre and Clobert 1995) RamasGIS/Metapop (Akçakaya and Root 2005), Prunus (Sebert-Cuvillier et al. 2009), BioMove (Midgely et al. 2010). There are demographic modelling packages for single-population in the open source statistical programming environment R (R Development Core Team, 2010): popbio (Stubben and Milligan 2007), Rramas (de la Cruz 2010). In the present software note we introduce the freely available R-package demoniche, which carries out spatially-explicit demographic modelling in sub-populations, with flexible options for dispersal, stochasticity and temporal trends in environmental suitability of the species niche. The model offers an efficient way to compare results between multiple repetitions and between different scenarios of change, to develop hypotheses concerning species persistence, fragmentation and range shift.

Basic functions

The demoniche package is a framework for spatially-explicit demographic modelling which simulates population growth for multiple sub-populations of a single species. The simulation method in each sub-population is a demographic transition matrix model (age- or stage-based). Demographic information can be obtained from long-term inventories or mark-recapture studies. For further explanations about demographic modelling please see subject

handbooks (Caswell 2001, Morris and Doak 2002).

The demoniche model runs stochastic simulations by selecting among different transition matrices that represent demographic responses to environmental or human impact scenarios, such as fires, clear-cutting, grazing, management actions, or climatic conditions. The matrices could also be calculated from vital rates obtained from different years of sampling (e.g. Hunter et al. 2011). During each time-step, the mean/reference transition matrix or the scenario matrix is randomly selected for matrix multiplication, according to a user-defined probability. There is also an option allowing the values in the transition matrix to be randomly varied according to a user-supplied distribution and variance matrix. These two processes (selecting a different matrix and varying the matrix rates according to the variance matrix) represent two types of demographic stochasticity. An option of specifying temporal autocorrelation in the matrix selections also exists, so that the probability of choosing the same matrix in subsequent yeas is decreased or increased. The demoniche model also provides the possibility of defining a maximum carrying capacity for each population.

Apart from demographic information, parametrizing the model also requires information about the initial geographical distribution of the modelled species, and there are various alternatives offered to the modeller. The demoniche model incorporates information regarding the geographical distribution of current and future environmental conditions, referred to as Niche values. The Niche values are connected to the demographic model and modify the elements of the transition matrix (either reproduction, survival or growth elements), as defined by the user. These values can represent any spatially distributed conditions that are thought to influence the suitability of the species' niche. Niche values can be obtained from Species Distribution Models, future climate scenarios from General Circulation Models (GCM), land use-change predictions, habitat cover types, landscape topology, etc. Niche values can include zeros if the surrounding landscape is completely unsuitable for the species. The demoniche model gives users the option to run demographic projections without changing the environmental suitability, to investigate effects on species persistence. The two sources of dynamic change (matrix selection and Niche values) can be used together and separately, according to the availability of information and purpose of the investigation.

The geographic distribution of the species is either patch- (islands, lakes, population patches, habitat fragments, protected areas) or grid-based (equal-sized cells). Dispersal between populations can be either short (with dispersal to the eight contiguous cells) or long-distance dispersal. The long-distance dispersal is modelled by an exponential dispersal kernel with user-defined constants according to the formula $P = a*exp(D^{c/b})$, with D = distance in kilometers between populations. These constants describe the shape of the species dispersal probability curve, and defines a maximum distance beyond which dispersal is impossible. Long- and short-distance dispersal can be applied separately or together, or simulations without dispersal can be run.

Sample usage

A manual and an example script that explains the possible values of each argument in the model is included in the package. The script shows step-by-step modelling for one example species and uses demographic data for *Hudsonia montana* (mountain goldenheather, Gross et al. 1998) from the popbio package, and hypothetical geographical distribution. The manual and example script also give suggestions of how to further visualize and analyse outputs.

Input data is either written directly into the workspace, or read from csv or txt files according to standard R procedures. The first step is to run the function '**demoniche_setup**' (Fig. 1), which checks the consistency of the user-supplied information and generates an R object containing the necessary information for modelling. The object is saved in the working directory for future reference.

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Secondly, the '**demoniche_model**' function (Fig. 2) performs the modelling simulations on the species object created by 'demoniche_setup'. In the 'demoniche_model' function the user specifies if she/he wishes to include effects of the Niche values and dispersal. The user also needs to specify how many modelling repetitions are to be carried out and supply a name for the folder where the simulation results will be saved. The 'demoniche_model' function runs two internal functions, '**demoniche_population**' that carries out demographic modelling in each population and year, and '**demoniche_dispersal**' that calculates the dispersal if selected.

Model Output

Various outputs are created from the modelling process. First, the output from the 'demoniche_model' function itself is an array containing the population sizes at each time step calculated from all repetitions: the mean, Expected Minimum Abundance (EMA, McCarthy and Thompson 2001), and standard deviation of mean population sizes (Fig. 2). The third dimension of the array is the different treatment matrices. Complete yearly population stage distributions from each repetition and each population are saved in the folder with the specified name. These data can be visually or statistically analysed, or exported to other formats for further analysis of population dynamics. The function automatically creates graphs of the EMA of each transition matrix treatment scenario, and maps of the occupancy throughout the modelled area, at each time step (Fig. 3).

The 'demoniche_model' function also computes demographic results from each transition matrix: the deterministic growth rate of the matrix, the stable stage distribution, sensitivity and elasticity matrices, the reproductive value of each life stage, and the damping ratio. These values are calculated by the function 'eigen.analysis' from the popbio R-package, for further information see the handbooks cited above. The function also saves a comma-separated file with the total initial range size, initial population size, percentage of populations that went extinct during the simulations, the growth rate (λ) of the scenario and the long-term stochastic growth rate calculated from the mean/reference and scenario matrices.

In conclusion, the demoniche package offers a framework for spatially-explicit demographic modelling. The model incorporates both biologically realistic demographic modelling (dispersal, density dependence, allee effects), as well as gradual changes and random fluctuations in the environment. In the demoniche framework it is easy for the user to change one parameter to explore effects of for example future environmental conditions, different probabilities of scenario matrix selection, increasing stochasticity, dispersal rates. The modelling results from different scenarios can be easily compared, facilitating uncertainty estimations and drawing attention to knowledge-gaps. Advantages of models created in R is transparency and adaptability to the specific modelling needs of the species and the modellers.
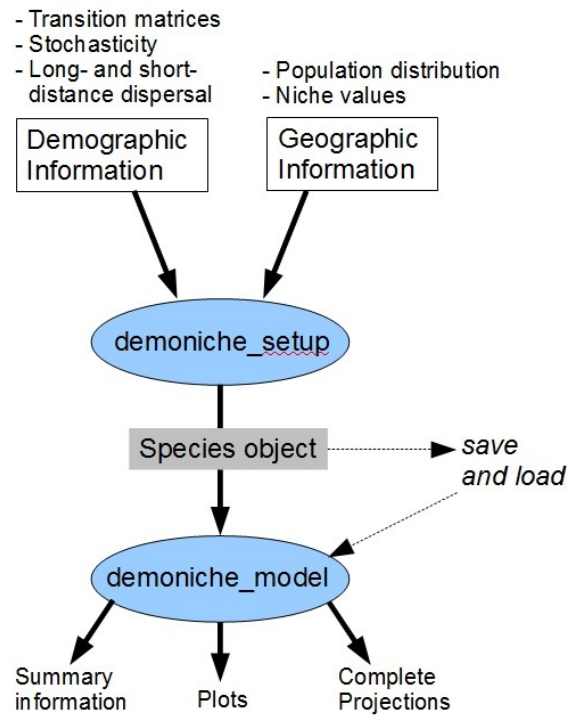
Available at:

How to cite demoniche:

Fig. 1. Simplified schema of the 'demoniche' framework. First the user enters demographic and geographic information into the 'demoniche_setup' function. A species object with all the necessary information is created, which is saved for future reference. The 'demoniche_model' function does the demographic modelling with the information in the species object. Summary results (e.g. average yearly population size) from the demographic modelling are created in the R-session, plots (Fig. 3) are generated, and complete yearly projections from each repetition and each sub-population are saved in the working directory.
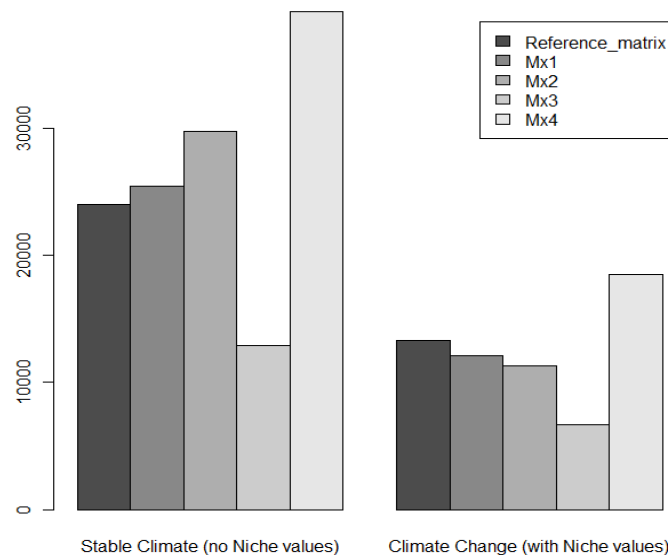
Fig. 2. Population size (number of individuals) for simulations using different treatment matrices, at the end of simulations. Including the effects of Niche values (in this example outputs from a Species Distrbution Model) there was a lower predicted population size.
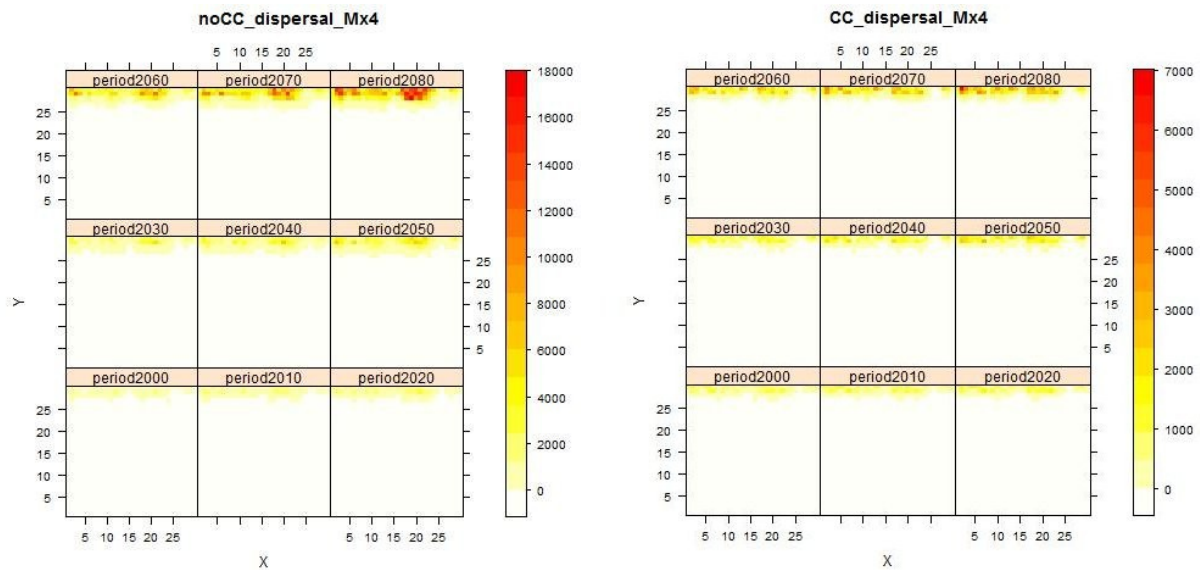
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Fig. 3. Map of populations occupied by the modelled species, under stable climate (left panel) and climatic change (right panel) with dispersal, during each time period of the simulation (2000-2080) for one treatment matrix. In this example the species' suitable niche moves downward. With climate change there was a lower predicted population size, and including dispersal caused the population to shift its range slightly downward. The intensity of the color indicates the population size in each grid cell. These graphs are automatically generated by the 'demoniche_model' function.

Acknowledgements

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