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Nemo-age: Spatially explicit simulations of eco-evolutionary dynamics in stage-structured populations under changing environments

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Abstract

1. Anticipating and preparing for the effect of environmental changes on biodiversity requires to understand and predict both the ecological and evolutionary responses of populations. Tools and methods to efficiently integrate these complex processes are lacking.

2. We present the genetically and spatially explicit individual-based simulation software Nemo-age combining ecological and evolutionary processes. Nemo-age has a strong emphasis on modelling complex life histories. We here provide a methodology to predict changes in species distribution for given climate projections using Nemo-age.

3. Modelling complex life histories, spatial distribution and evolutionary processes unravel possible eco-evolutionary mechanisms that have been previously overlooked when populations endure rapid environmental changes.

4. The interface of Nemo-age is designed to integrate species' data from different fields, from demography to genetic architecture and spatial distributions, thus representing a versatile tool to model a variety of applied and theoretical scenarios.

KEYWORDS
adaptation, forward-time simulations, life history, population dynamics, spatially explicit

1 | INTRODUCTION

Awareness of the effect of environmental changes driven by human activities on biodiversity is now established. Environmental changes are multifactorial with increasing population fragmentation and extinction risk (Guo, Lenoir, & Bonebrake, 2018; Urban, 2015). Anticipating and preparing for the effect of climate change requires to understand and predict how different factors affect the response of populations to these changes. A large body of theory and tools for predicting species responses has been built upon these premises (reviewed in e.g. Diniz-Filho et al., 2019; Urban et al., 2016), based on classical ecological and evolutionary theory.

The first tools attempting to predict the consequences of climate change on biodiversity and more specifically on species' ranges have developed from the concept of the Hutchinsonian ecological niche (Hutchinson, 1957) and resulted in so-called species distribution models (SDM; Elith & Leathwick, 2009) (or ecological niche models, ENM). An SDM is a static description of the current environmental requirement of a species (its niche), averaged across its current distribution (Elith & Leathwick, 2009). Coupled with environmental projections from climatic models, the niche model is then projected in space and time to provide a prediction of potential shifts of the spatial distribution of a species under different scenarios of climate change (e.g. Thomas et al., 2004). Yet, this approach has rapidly been criticized to not include basic biological properties of species such as dispersal propensity, demography or evolutionary processes, which can all strongly affect the predictions (e.g. Diamond, 2018; Hoffmann & Sgro, 2011; Lavergne, Mouquet, Thuiller, & Ronce, 2010). Progress

has been made in developing *hybrid* SDM to incorporate demographic and dispersal processes, unraveling new fundamental mechanisms (e.g. extinction debt Dullinger et al., 2012).

While recent niche projection methods refined the implementation of species ecology, only a few attempts have been made to implement evolutionary processes (Diamond, 2018). However, evidence is accumulating that climate change drives contemporary evolution of wild populations (see a review in de Meester, Stoks, & Brans, 2018). Theoretical investigations have long demonstrated that evolutionary processes are crucial to understand the contemporary responses of populations to environmental variation both in time (e.g. Gomulkiewicz & Houle, 2009; Kopp & Matuszewski, 2014; Lynch, Gabriel, & Wood, 1991) and space (e.g. Kirkpatrick & Barton, 1997; Polechová & Barton, 2015). These investigations, however, relied on simplifying assumptions on species ecology and genetics, providing strong conceptual advances but limiting their predictive potential in actual case studies. Among the main limitations, the above theory mostly ignored that many species have life histories with different stages and overlapping generations. Recent theoretical advances, however, showed complex interactions between life history and evolutionary dynamics when populations face environmental changes (Cotto & Ronce, 2014; Cotto, Sandell, Chevin, & Ronce, 2019; Orive, Barfield, Fernandez, & Holt, 2017). In addition, most models are deterministic or consider only part of the stochastic processes that can especially occur in small populations (genetic drift, Bürger & Lynch, 1995; Lande, 1993, for demographic stochasticity). Predictions on how sustained environmental changes challenge populations require the relaxation of most classical assumptions of theoretical studies.

Only a few studies have taken up the technical challenge of combining both ecological and evolutionary mechanisms in a single framework to predict changes in species distributions (Diamond, 2018; Urban et al., 2016). The first attempts to couple SDMs with evolutionary processes incorporated physiological responses of insects to temperature (Bush et al., 2016; Kearney, Porter, Williams, Ritchie, & Hoffmann, 2009). These models showed that evolution might play a crucial role in shaping the future range of short lived insects. However, these studies did not consider explicit demography (i.e. overlapping generations) and stochastic processes (genetic drift, demographic stochasticity), thus sharing some of the limitations of theoretical studies. While these choices can be justified by the time-scale of climate change relative to the generation time of the insect species considered and by their likely large population size, the above conclusions can hardly be extrapolated to other organisms. Recently, Cotto et al. (2017) coupled genetically explicit and life-history explicit individual-based simulations with SDMs to project the change of the range of perennial plants. The coupling of explicit demographic and evolutionary processes through time and space unravelled how, for long-lived species, the current species range does not reflect the demographic state and adaptation of local populations.

Here we present the software developed in Cotto et al. (2017), combining ecological and evolutionary processes. The core of the approach is an advanced eco-evolutionary model implemented in NEMO (Guillaume & Rougemont, 2006). NEMO is an already well developed individual-based simulation software with thoroughly tested evolutionary modules. We present the features of NEMO-AGE, a new version of NEMO that extends its capacities to stage-structured populations and allows for the modelling of a large variety of life cycles. In addition, we propose a method to forecast changes of species' ranges under climate change, where eco-evolutionary simulations are implemented from current species distributions as predicted with an SDM framework. NEMO-AGE can serve a diversity of both applied and fundamental uses related to the investigation of the spatio-temporal responses of populations to environmental changes. In this presentation we focus on its application to eco-evolutionary dynamics and evolutionary genetics in forward-time models of structured populations.

2 | MATERIALS AND METHODS

NEMO-AGE simulates the demographic and evolutionary dynamics of a network of stage-structured populations forward in time. It is based on NEMO (Guillaume & Rougemont, 2006), a platform for genetically and spatially explicit individual-based simulations. NEMO-AGE was designed to model life histories with multiple life stages and stage-specific selection pressures. Age structure is always nested into the stage structure in NEMO-AGE (age structure is a special case of stage structure). We develop these aspects of NEMO-AGE in detail below. Even though we recapitulate some of the most interesting features of NEMO, readers interested in the details of the original platform should consult (Guillaume & Rougemont, 2006), NEMO2 users' manual (http://nemo2.sourceforge.net). We first focus on the architecture of a simulation, presenting the different key modelling components. Then we provide details on the specific features of NEMO-AGE, and examples of how to combine them to build a modelling framework for eco-evolutionary forecasting.

2.1 | Architecture of a simulation

A simulation in NEMO-AGE assembles three main components: the population, a set of life cycle events (LCE), and the evolvable traits involved in adaptation to the environment. In NEMO-AGE, the LCEs allow to simulate stage-structured populations on large spatial scales. The population can be divided into subpopulations (hereafter patches) connected by dispersal.

The LCEs are operators that modify the state of the population and of the individuals, for instance by adding new individuals to patches (*breeding*), moving individuals among patches (*dispersal*) or stages (*aging*) or selecting surviving individuals depending on the expression of a genetically determined phenotype relative to a locally optimal trait value (*viability_selection*). The user chooses the sequence of LCEs executed within a time step (typically a year). The same sequence of LCEs is performed in each patch at each time step.

LCEs are executed independently within each local population. In principle, the sequence of LCEs can be matched to a matrix population model (accounting for dispersal), which is a useful feature for baseline comparison with analytical expectations (see Appendix A in Supporting Information and NEMO-AGE online user manual).

The traits modelled will typically be polygenic quantitative characters coded by additive quantitative loci (QTL) under stabilizing or directional selection. NEMO-AGE also incorporates previous genetic modules of NEMO, allowing for the modelling of neutral genetic variation (microsatellites or bi-allelic polymorphisms) and deleterious mutations under purifying selection.

2.2 | The key features of NEMO-AGE

NEMO-AGE is particularly intended to model eco-evolutionary dynamics triggered by spatio-temporal environmental changes (but also handles simpler situations).

2.2.1 | Stage-specific demography

Many organisms have several life stages that generate heterogeneity in the vital rates of individuals within a population (Caswell, 2001; Charlesworth, 1994). A correct description of the demography of these organisms requires to classify the individuals in life stages representing their heterogeneity. The age of an individual is tracked from birth. NEMO-AGE then lets the user define the number of life stages and the maximum number of years an individual can stay in each life stage (here we use year as a time unit for simplicity). Therefore, stages and ages can or cannot correspond, depending on the user's choice. There is no constraint on the number of ages or stages that can be implemented. The default minimum life cycle defined by the transition matrix has two stages, with offspring and adults, and non-overlapping generations.

NEMO-AGE uses a matrix as a parameter to describe the transitions between stages. The structure of the transition matrix is a fixed property of the modelled organism, in time and space (NEMO-AGE does not allow selection on the life cycle itself). The transition matrix in NEMO-AGE is thus a population parameter and is the same for all individuals (i.e. in all patches for all sexes). The transition matrix in NEMO-AGE must define all stages explicitly and distinguish between reproduction and probabilities of direct transition between stages (sensu Barfield, Holt, & Gomulkiewicz, 2011, as NEMO-AGE treats these life cycle events independently; see manual). It might thus not match directly with a transition matrix whose elements can compound survival and reproduction events (e.g. fertility and first year survival for a Leslie matrix, details are provided in the manual section 3.2.1).

Each year, every individual is tested through the screen of the transition matrix to determine its fate in the next year (i.e. remains in its stage, transits to another stage or dies). This is handled by a single LCE (*aging_multi*, see manual section 4.1). NEMO-AGE assumes that mating is random within local populations (LCE *breed*, manual section 4.2). The expected number of offspring from a mating event corresponds to the stage-fertility of the female. Clonal reproduction is an independent event not managed via the transition matrix (LCE *cloning*, manual section 4.3). It contributes individuals via non-sexual reproduction (i.e. produces an exact copy of an individual) to a user's defined stage in the life cycle. Lastly, natal dispersal is the default dispersal model (LCE *disperse*, manual section 4.4) but NEMO-AGE allows to model stage-specific dispersal.

The dynamic of the populations is thus modelled at the individual level and accounts for demographic stochasticity (Caswell, 2001, chapter 15). The number of individuals of each sex in each stage, as well as the total number of individuals can be monitored during simulations and provided as output statistics. A simple example of an implementation of a stage-structured model is provided in Appendix A in Supporting Information.

2.2.2 | Density dependence and population regulation

In natural populations, limited resources promote density-dependent competition. Within stage-structured populations, competitive interactions can affect the different life stages asymmetrically. For example, adults density can affect juvenile survival, while adult survival remains insensitive to juvenile density (e.g. in trees). In NEMO-AGE, we implemented two non-exclusive forms of regulation acting on survival probabilities. The first involves intraspecific competition using either Beverton and Holt (1957) or Ricker (1954) functions. The stages affected by intraspecific competition and the competitive weight of each individual determine the population size at equilibrium (see Section 3 and Appendix A in Supporting Information). Once the stages under competition have been identified, coefficients for the strength of competition on each stage can be adjusted to obtain the desired population size at demographic equilibrium. The second regulation model implements random ceiling regulation to maintain the patches below a desired carrying capacity acting as a threshold (the ceiling). This form of regulation can also be used to constrain the range of a population to an initial area on a grid by setting some of the patch carrying capacities to zero. It can also be used as a safeguard against transient bursts in population size that occur for example, if density competition affects a single stage. Regulation is handled by the LCE *regulation* (see manual section 4.7).

2.2.3 | Stage-specific selection and trait evolution

Selection is handled by a specific LCE, which can be placed anywhere in the life cycle (*viability_selection*, see manual section 4.5). Following classical approaches for modelling the evolution of quantitative traits in structured populations (Barfield et al., 2011; Lande, 1982; Lande & Arnold, 1983), NEMO-AGE assumes that stage-specific transition rates depend on a Gaussian relationship between the quantitative phenotype of the individual and an optimal phenotype. Selection on

fecundity can be implemented using selection on first year survival (see manual section 4.11.1). This way, the demography of the population is linked to evolutionary processes via the effects of natural selection on the different transitions between stages and thus on the population growth rate (see Appendix A in Supporting Information).

Any phenotype can potentially be implemented. NEMO-AGE can handle multivariate phenotypes and selection. In the case of modelling species distribution, the phenotype can be the (multivariate) environment itself, such that the optimal phenotype within a patch is the local environment (e.g. average temperature and precipitation, see Section 3). Temporal variation of the optimal phenotype (e.g. the environment) can be modelled by providing temporal series or per-year rate of change (see NEMO-AGE manual), for instance using climate change scenarios (Moss et al., 2010).

The strength of selection may depend on the stage of the individual. For example, juveniles are often more sensitive to the environment than adults. Moreover, some traits may be expressed and exposed to selection in certain life stages but not in others. NEMO-AGE allows modelers to account for such stage-specific selection on quantitative traits by specifying stage-specific selection parameters. The width of the Gaussian selection function is inversely related to the strength of selection on the phenotype. It can be specified separately for each stage and each trait under selection and can change during the course of a simulation, but does not vary in space (unless a single stage is under selection, see manual section 4.5.4).

2.2.4 | Trait architecture

Adaptation to local conditions is mediated by the evolution of quantitative traits. Multiple quantitative traits, and their genetics, can be modelled in NEMO-AGE. The population response to selection after an environmental change will then depend on how much additive genetic covariation is present at the traits concerned. Each individual can carry a suite of potentially correlated characters that are determined by a number of purely additive quantitative trait loci (QTL). NEMO-AGE models the genome of each individual explicitly. The QTL can be pleiotropic and affect multiple characters under selection. The number of loci and their position on chromosomes can be set by specifying a recombination map (in centiMorgans).

The additive genetic variation V_A at the trait(s) is determined by the mutation rate and the distribution of allelic effects, set either as fixed di-allelic values or random effects drawn from a multivariate Gaussian distribution. Clearly, access to estimates of such parameters is limited in practice and the choice of parameter values will lie primarily with the user. Estimates of V_A require trait measurements in individuals with known relatedness, for instance from common garden experiments or from pedigreed populations. Estimating V_A is thus challenging for wild, non-model species not easily raised in captivity or with long generation times (Gienapp et al., 2017). In many cases, the choice may depend on preliminary sensitivity analyses to establish the importance of genetic parameters (see Figure 2 for an example on the mutation rate).

In guiding choices of parameter values, several criteria must be taken into account. First, the computer resources required increase linearly with the number of loci an individual carries and the total number of individuals. Large simulations of the order of 10^6 individuals with 10–120 QTL per trait require 5–10 GB of RAM respectively (see Appendix B in Supporting Information). Second, in the absence of empirical estimates of genetic variance and co-variance between traits, general guidelines based on quantitative genetics theory can be followed to parameterize the genetics of the traits. For example, the mutation rate (μ) and allelic variance (α^2) can be set to reach a total mutational variance of the trait equal to $V_m = 2L\mu\alpha^2$, for L QTLs. The total amount of additive genetic variance V_A, if known, can be reached at mutation-drift-selection equilibrium based on V_m, the strength of stabilizing selection and environmental variation $V_S = \omega^2 + V_E$ (ω^2: width of the Guassian selection surface; V_E: environmental variance of the trait), and the effective population size N_e, following the 'stochastic house-of-card' expectation, when the mutational variance is larger than the mutation rate: $V_A = \frac{2N_e V_m}{1 + (N_e \alpha^2 / V_S)}$ (Bürger, 2000). Estimates of the per-locus mutation rate and mutational variance have been extensively discussed in the literature (e.g. Bürger & Lande, 1994; Sella & Barton, 2019, and references therein). The relationship between the different components of variance V_m, V_E and V_S has been discussed in Turelli (1984), and Johnson and Barton (2005). We provide further guidelines and benchmarking on genetic parameters in Appendix C in Supporting Information.

2.2.5 | Explicit space

The spatial setting corresponds to a geographic map divided into patches (cells) to form a grid. The number of patches that (equally) divide the grid depends on the user's choice and defines the spatial scale of the model (surface area covered by each patch). The environmental or climatic model used to set the environmental values within each patch needs to correspond to the chosen spatial scale. Each patch potentially holds a number of individuals (i.e. a population) depending on the demographic (e.g. dispersal) and evolutionary (viability selection) processes. Patches are connected by dispersal and possibly subject to random extinctions (metapopulation; Levins, 1969).

NEMO-AGE benefits from previous features of NEMO with an efficient management of several dispersal models by a dedicated LCE (see manual section 4.4). The modelling of dispersal is highly flexible, including sex-specific dispersal or changes in dispersal probabilities (connectivity) over time. In addition, NEMO-AGE implements an efficient way of handling dispersal on very large spatial grids (>1,000 patches) with spatially limited dispersal. Geographical distances are abstracted out by only providing matrices of patch connectivities and pairwise dispersal probabilities between connected patches based on the dispersal kernel of the species modelled. To prevent building very large sparse dispersal matrices, pairwise patch connectivity and dispersal probability matrices can be specified for the connected patches only.

2.2.6 | Flexibility

NEMO was built in C++ with a modular software architecture. Most simulation elements, especially the individual traits and life cycle events are facultative and can be omitted. The LCEs that occur within a year can be placed in any order, for instance to apply viability selection on juvenile before or after dispersal or regulation, and thus model soft or hard selection. Specific LCEs have been created to optimize the life cycle of certain life histories and avoid having to produce too many offspring with little chance to survive, for instance. Such an LCE is provided for the life cycle of the perennial and clonaly reproducing plants modelled in Cotto et al. (2017).

Additionally, the parameter values of the different LCEs can be changed during a simulation at times specified by the user. This way, the population structure, the patch connectivity, the strength of selection or the local phenotypic trait optima can be changed to model temporal changes in patch occupancy or climatic conditions. Specific parameters are also provided to model constant gradual changes of the local conditions.

3 | RESULTS

We provide an example demonstrating how NEMO-AGE can be used to investigate the ecological and evolutionary responses of a species to a changing environment within a spatially explicit framework. The example is primarily intented to (a) emphasize the main features of NEMO-AGE and (b) propose a general method to combine species data with simulation components to project changes in species' range under climate change scenarios. Emphasis will be on methodology rather than on biological conclusions, which have been fully developed elsewhere (Cotto et al., 2017). Along the way, we will further propose solutions to issues that can occur as a result of a lack of estimates for some parameters. The files and code for the simulation are provided in an online repository (see Section 'Data availability statement').

3.1 | Stage-specific demography

We will focus on the response of the two alpine plants *Campanulla pulla* L. and *Dianthus alpinus* L., endemic to the Austrian Alps, to the projected climate change. For both species, we modelled a life cycle with four stages: seeds, seedlings, preadults and adults. Below, we provide the transition matrix parameter (M) where fecundities (i.e. the first row) correspond to the number of seeds from sexual reproduction.

$$M = \begin{pmatrix} s_0\left(1-g_r\right) & 0 & 0 & F_{ad}f_{fl} \\ g_r & 0 & 0 & 0 \\ 0 & s_{sdl} & 0 & 0 \\ 0 & 0 & s_{prea} & s_a \end{pmatrix}.$$

The cloning rate cl_r is independent from the transition matrix in the parameter file from which adult individuals contribute asexually to the seedling stage. The biological significance and values for parameters are given by

Parameter	Significance	*Campanulla pulla*	*Dianthus alpinus*
s_0	Survival in the seedbank	0	0.33
$F_{ad} \cdot f_{fl}$	Seed yield × flowering rate	96	9.6
g_r	Germination rate	0.165	0.165
cl_r	Cloning rate	0.5	2.6
s_{sdl}	Seedling survival rate	0.71	0.71
s_{prea}	Pre-adult survival rate	0.71	0.71
s_a	Adult survival rate	0.7	0.7

The parameter values are from Dullinger et al. (2012), Hülber et al. (2016) and Cotto et al. (2017). *Dianthus* differs from *Campanulla* essentially by producing less seeds from sexual reproduction, but those seeds can remain in a seedbank. *Campanulla* produces large quantities of seeds that do not survive over winter.

The succession of life cycle events in the life cycle as specified in NEMO-AGE parameter file is:

breed	1	*# with random mating and hermaphroditism*
disperse	2	*# with seed dispersal, affects only stage 0*
cloning	3	*# adds individuals to stage 1 − seedlings*
regulation	4	*# density dependent regulation with BH competition function*
save_stats	5	*# census time*
viability_selection	6	*# on stage 1 − seedlings*
aging_multi	7	*# stage transition*

3.2 | Population regulation

We implemented density regulation on seedlings that suffer competition from established adult plants within patches. We used the Beverton–Holt (BH) density-dependence model. We determined the competitive weight of individuals of both species, corresponding to the competition coefficient in the BH model, by simulating a single population and adjusting the competition coefficient to reach a difference in equilibrium population size between the two species proportional to the one expected from Dullinger et al. (2012, and see Appendix D in Supporting Information). Finally, we used the dispersal kernels of the seeds determined by Dullinger et al. (2012) (and used in Cotto et al., 2017) to build NEMO-AGE dispersal parameters (i.e. the patch connectivity matrix and the dispersal probability matrix).

3.3 | Space and environment variables

Once the biology of the species is determined, the next step is to define the study area and the relevant environmental variables. For our example, we selected a 64 km^2 area within the Austrian
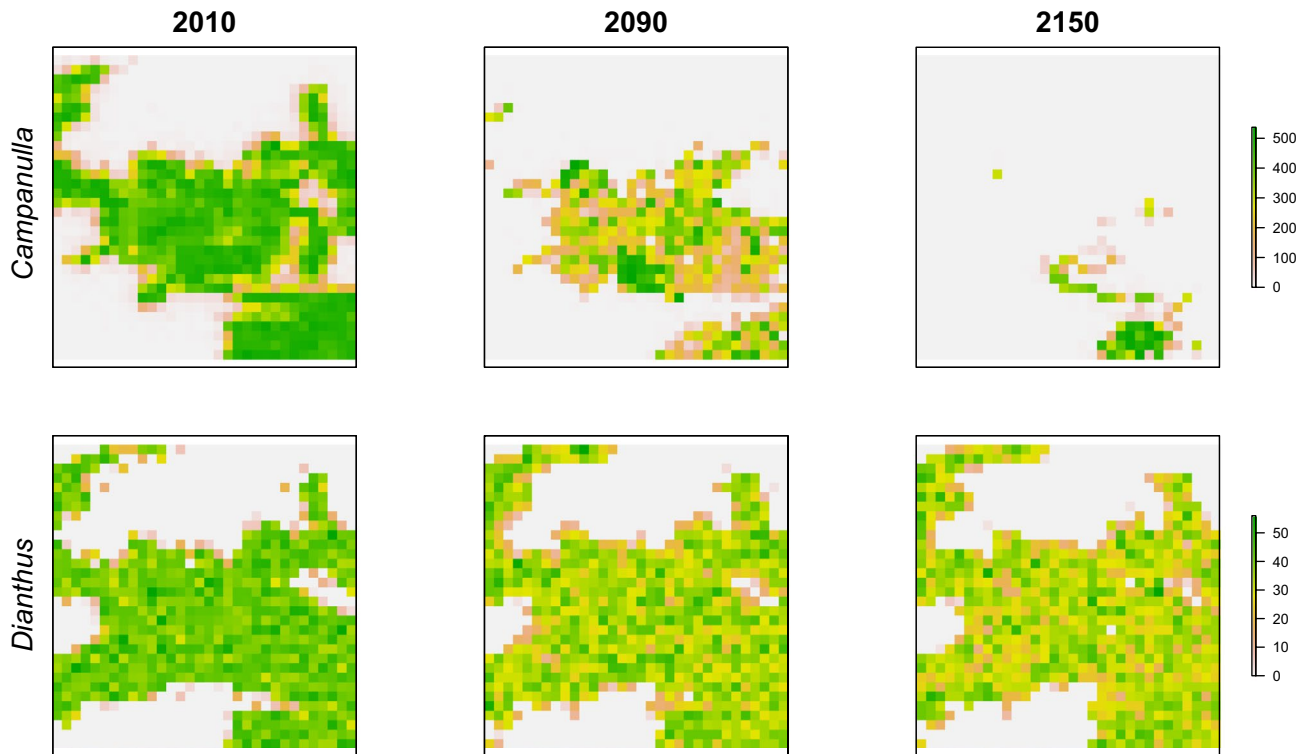
FIGURE 1 Distribution and size of the populations within the studied area at different year for the two species *Campanulla pulla* (top) and *Diathus alpinus* (bottom). Projections for future climate start in 2011 and finish in 2090. Therefore, distributions in 2010 and 2090 correspond to those prior and after (projected) climate change. Illustration for a single replicate for adult survival $s_a = 0.7$, mutation rate $u = 0.0001$, climate change scenario RCP 2.6. Colour scales are on the right represent number of individuals per cell/patch

Alps. The area is divided into a grid of 32 × 32 patches (i.e. 250 m scale; Figure 1). We then used the ensemble modelling framework Biomod2 (Thuiller et al., 2016) to obtain a map of the probability of occurrence of the focal species, based on presence–absence observations and environmental variables (see Figure 1, 2010). We used two WorldClim bioclimatic variables (http://www.worldclim.org) representing the mean amount of precipitation (BIO12) and the mean annual temperature (BIO1), and the abundance of carbonate in the soil (strongly structuring plant populations) as a non-climatic environmental variable. We considered that the species was present in a given patch when its probability of occurrence was above a threshold value (provided by the Biomod2 output, see Cotto et al., 2017). The SDM was run over the whole species range in the Austrian Alps at the 250 m scale. We used that output to set the initial distribution of occupied patches in our grid.

3.4 | Stage-specific selection

Climate mainly affects survival of the early stages, that is the seedlings in our model (see Cotto et al., 2017). The following step thus requires to define the relationship between Gaussian selection on seedling survival and the environment. In the current example this relationship is unknown. We propose that the phenotype of an individual is its climatic niche and that the optimum of the Gaussian selection function is the current environment. Therefore, an individual performs best

when its niche, that is, its phenotype, matches the current environment. We thus considered a three-trait phenotype, each trait corresponding to one of the three environmental variables we used in the niche modelling framework (see previous paragraph). To complete the selection model, we suggest that a baseline value for the width of the Gaussian selection function (inversely related to the strength of selection) can be obtained by estimating the environmental variation contained within the species' range as predicted by the niche modelling framework. We used the observed variance of each environmental variable as the lower bound to the strength of selection acting on the corresponding phenotypic trait in the seedlings. A sensitivity analysis, investigating several stronger selection intensities than this baseline is then required (see below). Lastly, we assumed that each trait in the multivariate phenotype is controlled by 10 unlinked additive loci.

3.5 | Sensitivity analysis

Importantly, modelling eco-evolutionary dynamics at the individual level requires to implement parameters for the different components of the simulations that might not be available for the case under study. Uncertainty on some parameters can add to the variation generated by the random processes within simulations (e.g. genetic drift, demographic stochasticity) and lead to a range of possible outcomes. This potential issue can be resolved using sensitivity analysis on the parameters that have been identified as key. For the present illustration, we

ran simulations over two different mutation rates, a parameter conditioning the potential evolutionary response fuelled by standing and de novo genetic variation. Further sensitivity analysis related to this example can be found in Cotto et al. (2017).

3.6 | Simulation setup

The last step for performing eco-evolutionary projections of the change in species' range is to integrate climatic projections of the future environment into the simulation framework. Assuming that the phenotype of the individual is its climatic niche, climate projections can be directly used as projections for the future phenotypic optima. Such climate projection are available from the International Panel on Climate Change (Moss et al., 2010) and need in general to be downscaled to the spatial scale of the study. We used here climatic projection as formatted for Cotto et al. (2017). Climatic projections are often available for time intervals larger than a single year (the time-scale of simulations), so that climatic projections need to be extrapolated within these intervals. Nemo-age allows linearizing climatic projections by implementing a linear rate of environmental change between two projections and by allowing this rate to be updated at any given year.

At this point, all the elements for performing species' range projection using Nemo-age are set. We advise to perform burn-in simulations prior to modelling the environmental change to reach both genetic and demographic equilibrium. In our example, burn-in simulations are initiated with the spatial distribution predicted from the niche modelling framework. The initial phenotype of each individual depends on the current environment within their cell. We thus assume that the populations are initially perfectly adapted to their local environment. The phenotypic and genetic variation around the trait optimum values should reach their migration-selection-mutation-drift equilibrium during burn-in. During burn-in, we further set null carrying capacity in cells outside the initial range predicted by the niche model to avoid colonization outside the initial range. In each occupied cell (within the initial range), the equilibrium population size depends on density dependence (which is identical for all cells, see Population regulation) and on the genetic load at equilibrium. Burn-in lasts for 5,000 generations. Five replicates were performed for each parameter set in the burn-in simulations and then used to initialize the climate change simulations. These simulations assume that the environment starts to change in 2010 (the first climate projection is for 2020) until 2090. We then kept the environment constant for 60 generations, to investigate the fate of populations in this best case scenario. Nemo-age can save statistics for the demographic and evolutionary state of the population, providing rich information from the scale of the species range (Figures 1 and 2) to individual genetics (Figure 2).
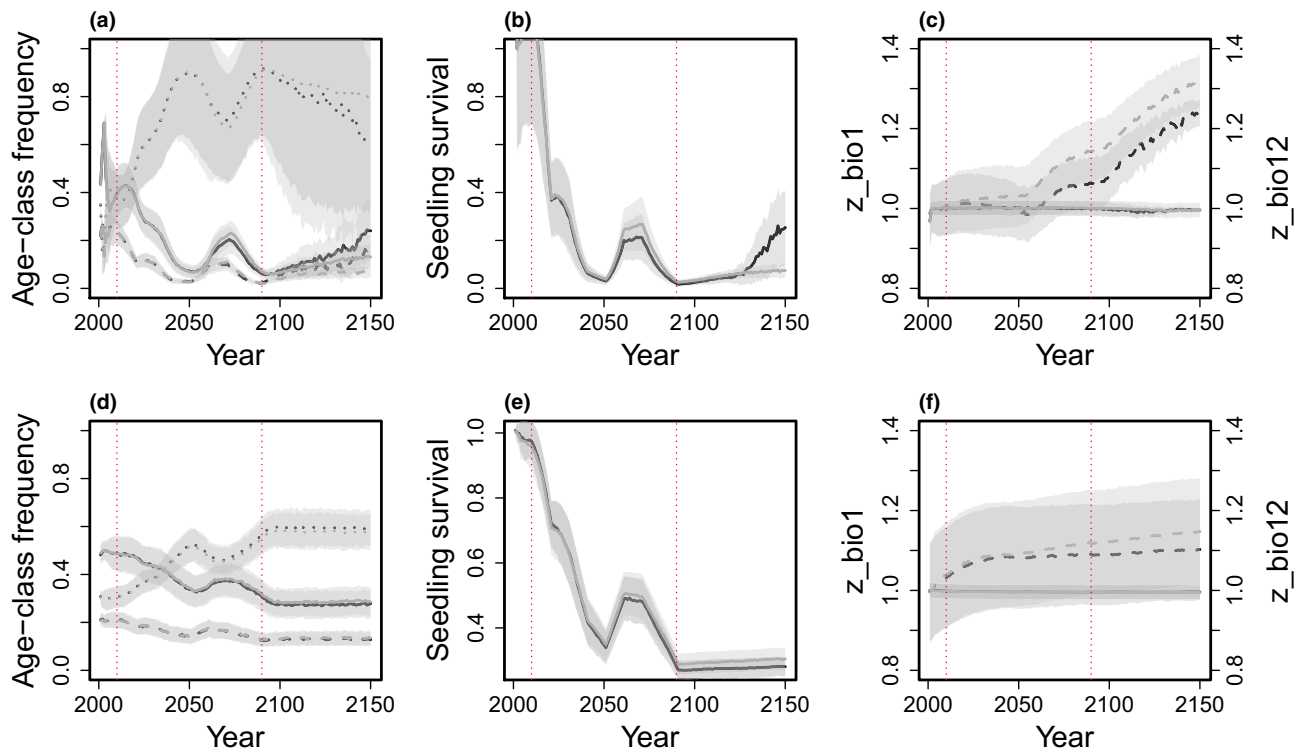

FIGURE 2 Age structure (a, d), seedling survival (b, e) and quantitative trait value (c, f) as a function of year for *Campanulla pulla* (a, b, c) and *Dianthus alpinus* (d, e, f). Panels (a) and (d), dotted lines: seedlings; dashed lines: pre-adults; full lines: adults. Panels (c) and (f), dashed lines: z_bio1 (mean annual temperature); full lines z_bio12 (annual amount of precipitation). Projections for future climate start in 2011 and finish in 2090 (vertical red dotted lines). Illustration for a single replicate for adult survival $s_a = 0.7$, mutation rate $u = 0.0001$ (black) and $u = 0.0010$ (grey), climate change scenario RCP 2.6. Lines represent the mean across all populations (occupied cells in the landscape), and the shaded area represents the standard deviation

4 | DISCUSSION

Nemo-age is a highly efficient and feature-rich individual-based simulation software designed to model both evolutionary and ecological processes that can occur on contemporary time-scales (micro-evolution). Nemo-age focuses on the evolution of quantitative traits in a spatially explicit context and in organisms with complex life cycles (see CDMetaPOP, Landguth, Bearlin, Day, & Dunham, 2017 and Metapop, Soularue, Thöni, Arnoux, Le Corre, & Kremer, 2019, for simulation tools focusing on different aspects). Nemo-age is a command-line tool with a simple parameter-file interface that does not require programming skills (see SLiM, Haller & Messer, 2019, for a different choice of interface).

The National Cancer Institute's Genetic Simulation Resources (https://popmodels.cancercontrol.cancer.gov/gsr/) provides a simulator repository and comparison tool. Among the currently available simulation softwares referenced therein, very few can handle forward-time simulations encompassing both evolutionary and ecological processes simultaneously. Indeed, forecasting changes in species' distributions while taking into account these processes is one of the computationally most challenging modelling exercises. In addition to the implementation of processes, the software should be able to allow for flexibility in data inputs to describe realistic spatial distributions of populations and of the environments, or the dispersal kernel of the focal species. We illustrated how Nemo-age combines all these features and can be coupled with SDM projection tools to tackle such a challenge. A thorough description of the features of Nemo-age is available in the comprehensive user manual. Another key characteristic of Nemo-age is that input formats are similar to those used in related fields, which eases the setting of simulations from existing data or for comparison with analytical theory. For instance, life-history settings are defined similarly to matrix population models (Caswell, 2001), which allow researchers to directly use large databases such as Compadre or Comadre (Salguero-Gómez et al., 2015, 2016). The Gaussian selection model for quantitative traits implemented corresponds to what is assumed in most theory on the adaptation of populations to environmental change (Kopp & Matuszewski, 2014) and to what is classically measured in natural populations (Chevin, Visser, & Tufto, 2015; Lande & Arnold, 1983).

While Nemo-age allows for the modelling of eco-evolutionary processes explicitly, some simplifying assumption have to be made to keep the level of complexity reasonable. Nemo-age is designed to prioritize investigations on how variation of the environment in time and space affects individual variation in life-history traits, and the subsequent demographic and evolutionary dynamics. Life history is implemented as a single matrix representing the expected transition probabilities between stages in the absence of selection. The transition matrix is assumed to be the same for all individuals. Natural selection affects transition probabilities at the individual level (i.e. depending on individual phenotypes relative to an optimum value) at any stage, but independently of the sex of the individual (see Connallon, Sharma, & Olito, 2019, for sex-specific effects

of selection). Therefore, all dynamics are driven by natural selection only, without density or frequency dependence. Nemo-age can model density-dependent regulation within populations that does not result on direct selection on the trait. Furthermore, the choice of the mutation model can affect predictions. For example, under a continuum-of-allele mutation model, there is no limit to the value of the traits. Therefore, a population can potentially adapt to any environment and expand indefinitely (Barton, 2001). A limit to the values traits can be set using a di-allelic mutation model. Adaptation to a new environment can also be facilitated by adaptive plastic phenotypic changes. Phenotypic plasticity is not part of this first release of Nemo-age (but see the Metapop software: Soularue et al., 2019). Finally, the possibility of species interactions is not implemented in Nemo-age. Species interactions can be positive (facilitation) or negative (predation, competition) and have been demonstrated to play an important role in shaping species' ranges, (Harley, 2011; Louthan, Doak, & Angert, 2015) especially where environmental stresses are mild (Louthan et al., 2018). This aspect of species biology needs to be anticipated when designing the simulation study and interpreting predictions.

Lastly, the development of simulation tools like Nemo-age to model stochastic eco-evolutionary dynamics in complex environmental scenarios trades off with increasing need in parameter values and computational resources. Among the main difficulties, one needs to know the strength of selection relative to the amount of (additive) genetic (co-)variance related to the study traits (Gienapp et al., 2017), which are crucial to the evolutionary dynamics. Rough estimates can be drawn from previous reviews (Johnson & Barton, 2005; Kingsolver et al., 2001), but patterns of genetic (co-)variances and selection could drastically vary in time and space (Nemo-age can handle spatial and temporal variation in the strength of selection). Genomics studies increasingly support the assumption that quantitative traits are under the control of a large number of loci (Gienapp et al., 2017), but deviations from this state can dramatically affect adaptive dynamics (Gomulkiewicz, Holt, Barfield, & Nuismer, 2010). On the other hand, approaches based on quantitative genetics theory that require less parameters (e.g. trait heritability) to assess how adaptation might affect the change in species range under climate change neglect potentially key processes such as stochasticity or feedbacks between stage-structured demography and adaptation (e.g. Bush et al., 2016; Diniz-Filho et al., 2019). The refinement of the evolutionary model eventually depends on the need of the study. Life-history parameters require estimates of transition rates between stages, which are available for an increasing number of species (e.g. Salguero-Gómez et al., 2015, 2016). Studies at larger taxonomic scales can perform sensitivity analysis on life history itself by drawing into a range of possible values (e.g. Pearson et al., 2014, but without evolution). Life-history estimates from natural populations, however, likely comprise different genetic loads resulting for example from dispersal from populations adapted to different environments, or from maladaptation (e.g. Lande & Shannon, 1996). Ideally, implementations of life-history models should account for these effects. Overall, in our example, we provide

a method to circumvent some of the difficulties arising when data are not directly available, but limitations related to availability and quality of data should always be kept in mind. To finish, we would like to point to the fact that, despite substantial effort for performance optimization, modelling both evolutionary and demography dynamics in space and time can require large computing resources (see Appendix B in Supporting Information), calling for further optimization of choices on the side of the operator.

AUTHORS' CONTRIBUTIONS

All authors contributed to developing NEMO-AGE from existing NEMO, writing NEMO-AGE manual and the present manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The code and parameter files used in the present manuscript, as well as the users' manual are available online at: https://zenodo.org/record/3961683. Note that the code version on Zenodo is 0.29.0 (git version tag) and is not updated. The software is developed on the public git repository https://bitbucket.org/ecoevo/nemo-age-release.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.