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Simulating plasticity as a framework for understanding habitat selection and its role in adaptive capacity and extinction risk through an expansion of CDMetaPOP

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Abstract

Adaptive capacity can present challenges for modelling as it encompasses multiple ecological and evolutionary processes such as natural selection, genetic drift, gene flow and phenotypic plasticity. Spatially explicit, individual-based models provide an outlet for simulating these complex interacting eco-evolutionary processes. We expanded the existing Cost-Distance Meta-POPulation (CDMetaPOP) framework with inducible plasticity modelled as a habitat selection behaviour, using temperature or habitat quality variables, with a genetically based selection threshold conditioned on past individual experience. To demonstrate expected results in the new module, we simulated hypothetical populations and then evaluated model performance in populations of redband trout (*Oncorhynchus mykiss gairdneri*) across three watersheds where temperatures induce physiological stress in parts of the stream network. We ran simulations using projected warming stream temperature data under four scenarios for alleles that: (1) confer thermal tolerance, (2) bestow plastic habitat selection, (3) give both thermal tolerance and habitat selection preference and (4) do not provide either thermal tolerance or habitat selection. Inclusion of an adaptive allele decreased declines in population sizes, but this impact was greatly reduced in the relatively cool stream networks. As anticipated with the new module, high-temperature patches remained unoccupied by individuals with the allele operating plastically after exposure to warm temperatures. Using complete habitat avoidance above the stressful temperature threshold, habitat selection reduced the overall population size due to the opportunity cost of avoiding areas with increased, but not guaranteed, mortality. Inclusion of plasticity within CDMetaPOP will provide the potential for genetic or plastic traits and 'rescue' to affect eco-evolutionary dynamics for research questions and conservation applications.

KEYWORDS

agent-based model, behavioural plasticity, CDMetaPOP, computer simulations, eco-evolutionary model, genotype-environment associations, habitat selection, *Oncorhynchus mykiss gairdneri*, temperature selection

1 | INTRODUCTION

Phenotypically plastic traits may result in constitutive changes in morphology by alteration of developmental pathways or by transient changes in physiology (e.g. thermal acclimation) or behaviour. Plasticity is complex because it can be either reversible or irreversible and may occur across generations (Pigliucci, 2001; Galloway & Etterson, 2007). Behavioural plasticity may occur in response to changes in the environment with regard to habitat selection, including breeding and foraging habitats, and has been observed across a wide variety of taxa (Clément et al., 2021; Gilbert et al., 2017; Morelli, 2012). Behavioural responses may be conditioned by past experience, whereby a stimulus elicits a fixed response after the first experience (e.g. predator avoidance) or the response may become muted over time after initial exposure. Because of this, behaviour itself can be considered a type of plasticity, in addition to physiological and morphological plasticity (Westneat et al., 2010). This genotype–environment interaction may experience lags in time to expression in reversible or irreversible traits (Forsman, 2015; Miner et al., 2005). Another important aspect of plasticity is that it may itself evolve through changes in norms of reaction, whereby expression of traits in a given environment differ among genotypes. For example, genotypes may differ in threshold values of cues inducing a plastic response or even in the direction of the response. Key responses that may affect fitness in changing environments include dispersal responses in relation to internal cues, habitat quality related to abiotic (e.g. thermal conditions) or biotic factors (e.g. presence of predators or competitors, including introduced species). Plasticity may express as habitat selection (Donohue, 2003), which can facilitate species distribution shifts in changing environments and/or ecological speciation (Nonaka et al., 2015).

Plasticity may play an important role in the adaptive capacity of species (Beever et al., 2017). Adaptive capacity is the ability of a system to persist in the face of environmental change, and understanding the adaptive capacity of species will drive the ability to conserve species increasingly impacted by climate change (Beever et al., 2016; Thurman et al., 2020). One important piece to understanding adaptive capacity is to be able to evaluate adaptive potential, dispersal and phenotypic plasticity in tandem (Seaborn et al., 2021). Adaptive capacity can determine the potential of populations to respond to environmental changes, yet neither adaptive genetic variation nor plasticity are commonly incorporated into models forecasting a species population response (Funk et al., 2019).

Consequently, there is a need for spatially explicit simulation software to assess the evolution of plasticity in changing environments (Scheiner et al., 2020). Spatially explicit models for plasticity are necessary to capture realistic spatial heterogeneity in habitat quality and patterns of selection and to account for natural or anthropogenic limits on dispersal. Methods for understanding plasticity also need to allow for temporal variation in the environment, including effects of climate change (Day et al., 2019). Because of these complexities, individual-based models are an excellent framework to integrate factors related to adaptive capacity and evolution, including plasticity, although currently there is not a framework to evaluate, for example the impact of plasticity on demography in conjunction with natural selection on alleles that may confer thermal tolerance. One approach for these models is through forward-time simulations, which historically have allowed users to simulate a wide number of parameters and scenarios for various systems (Yuan et al. 2012). Through simulations, one can iteratively evaluate which parameters are the most important for the question at hand such as population sizes or genetic signature responses (Day et al., 2018). Selecting the duration of the simulations can be challenging and be affected by the relevant time horizon of the research question or computational power (Hoban et al., 2012; Yuan et al., 2012), so pilot simulations may be necessary to determine the time for equilibrium either in allele frequencies or population sizes.

Cost-Distance Meta-POPulation is one existing demo-genetic (demographic and genetic) individual-based model platform which can evaluate dispersal and adaptive potential of a species, and allows researchers to then better understand adaptive capacity by modelling eco-evo feedbacks (Landguth et al., 2017; Seaborn et al., 2021). In addition to allowing for the simulation of dispersal and demographic processes, CDMetaPOP can also be used to simulate multilocus selection under a spatially explicit framework (Landguth et al., 2020). CDMetaPOP has been used for a wide range of simulation studies, including research questions centring on reproduction, dispersal, hybridization, translocation, natural selection, invasive species management and gene flow (Day et al., 2018, 2020; Escalante et al., 2018; Menon et al., 2020; Mims et al., 2019; Nathan et al., 2019). In this manuscript, we introduce a new module to expand the existing CDMetaPOP framework to fill a gap in the computational tools available to researchers interested in integrating phenotypic plasticity alongside spatially explicit models of traditional genotypic selection across the landscape.

Here, we describe the major features of a fixed behavioural plasticity module for habitat selection which also well-represents other fixed responses to environmental conditions, for example developmental plasticity. We show two examples that illustrate the new module under (1) a hypothetical landscape and (2) an empirical system using redband trout (*Oncorhynchus mykiss gairdneri*). Trout present an appropriate case study, because habitat selection can be temperature-dependent (e.g. behavioural thermoregulation at high environmental temperatures; Ebersole et al., 2001) and thermal preference may also shift with prior temperature experience (Baird & Krueger, 2003; Petty et al., 2012). In other fish species, physiological acclimation temperature, one form of individual experience, shifts temperature preference in laboratory settings (Hofmann & Fischer, 2002) and rainbow trout have been shown to have an interaction between behavioural plasticity and temperature (Baird & Krueger, 2003; Frost et al., 2013). In the redband trout simulations, as a simulation proof of concept, we tested simulations with a thermal tolerance allele, an allele for the plastic response, the two of them together, and scenarios where neither were present. In the simulations we present, the allele for the plastic response was tied to the temperature of the patches, and so represents a thermal preference plastic allele. The simulations demonstrated avoidance of poor-quality patches, that the expression of the plastic trait varies with the proportion of patches above the triggering temperature, and that plasticity in habitat selection behaviour based on past, individual experience resulted in higher average individual survival, but lower overall population abundance. The empirical proof of concept simulations also sets the foundation for future studies focused on the aforementioned processes in a spatially explicit framework. Lastly, we discuss the specific advantages and opportunities for applied simulations that the new module in CDMetaPOP provides.

2 | METHODS

2.1 | Simulation program

The behavioural plasticity for habitat selection module was built upon the existing framework of the individual-based landscape demo-genetics program, CDMetaPOP v1.71 (Figure 1). CDMetaPOP simulates genetic exchange and population dynamics for spatially referenced individuals on a resistance surface, a raster map of the ability for an organism to move (Garroway et al., 2011), where mating and dispersal events are a probabilistic function of effective or ecological distance between locations. Past versions of CDMetaPOP (e.g. Landguth et al., 2020) modelled natural selection via multilocus adaptive variation and multivariate environmental selection. Here, we extend the model's evolutionary processes to include behavioural plasticity which may 'switch' the habitat preference threshold and thus the agent's responses to local environmental cues during the remainder of the life cycle. The new module is implemented within the population parameter input file and draws habitat information from the spatially explicit patch file (see Table S1 for description of new parameters).

2.2 | Behavioural plasticity module

Each simulated individual is diploid, with a single locus encoding plasticity as present or not with a '1' being the allele for the plastic response and '0' being the allele for not having the plastic response. Individuals with the plastic allele are further coded as possessing the allele in an uninduced state of the trait ('1') or as possessing the allele in the induced state ('2'). In the present model, habitat selection behaviour related to patch habitat quality or temperature is induced by past experience of a patch above a habitat or temperature threshold. This induction threshold is defined by the user and implicitly represents one locus or multiple linked loci. We note that within the code, the switch of an allele

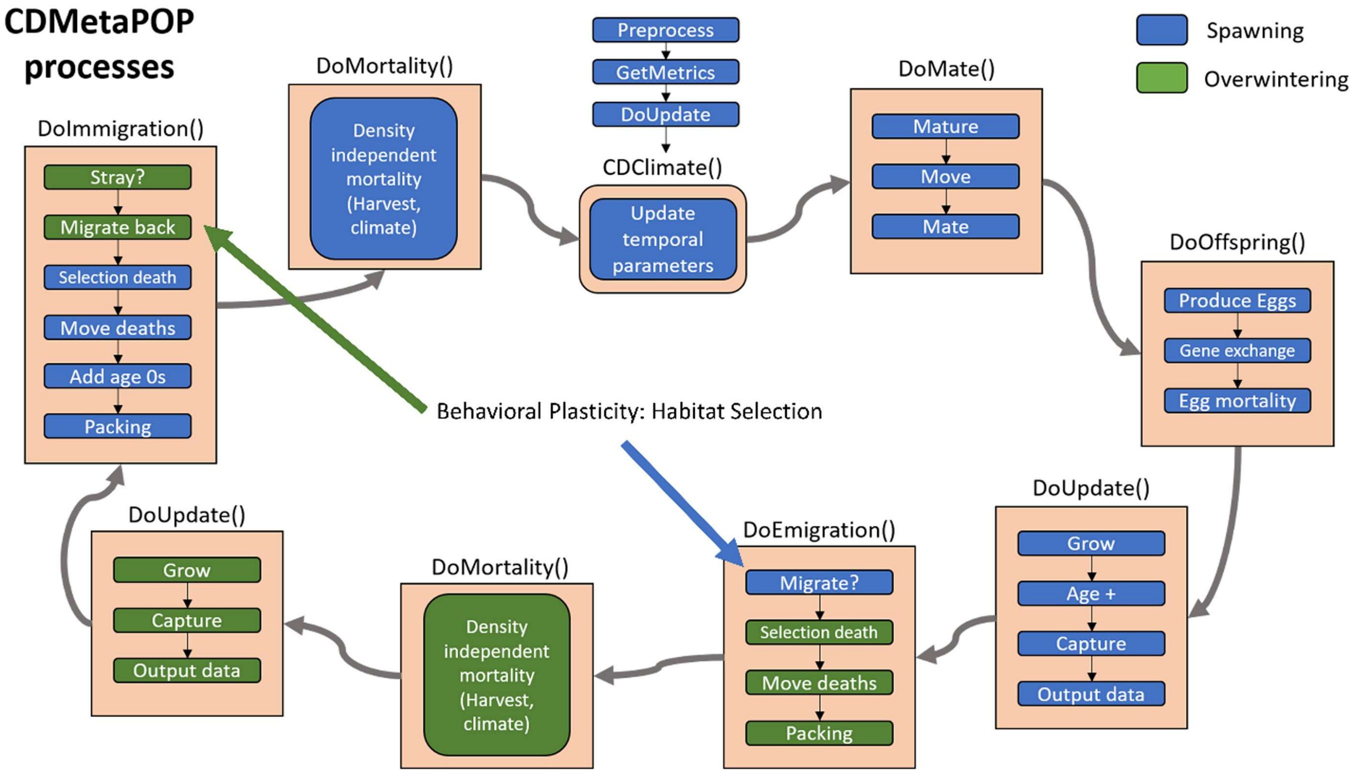


FIGURE 1 Location of habitat selection model within CDMetaPOP. Arrows and text of new module show where the habitat selection fits within CDMetaPOP and the original diagram. Original diagram from CDMetaPOP documents with full explanations of module processes available at: https://github.com/ComputationalEcologyLab/CDMetaPOP/tree/master/doc. Note that selection is implemented as mortality, and not fecundity.

from ‘1’ (plastic allele, not induced) to a ‘2’ (plastic allele, induced) is used for tracking the induction state of the plastic response but does not represent a new allele or, consequently, a true new genotype for the individual.

In our example redband trout model, the induced state results in habitat selection during seasonal migration events by using a reduction to the existing CDMetaPop probability matrix, which occurs during the emigration and/or immigration steps during seasonal migration (Figure 2). Initial frequencies of each plastic allele are user defined as ‘0’ or ‘1’. In our diploid model, the plastic allele will be induced if an individual exceeds the temperature or habitat threshold, and both alleles are induced if an individual is homozygous for the plastic allele. We treated the plastic response as dominant in our simulations, and therefore, heterozygotes exhibit the plastic trait when induced. However, users of the module may select whether the response is dominant, recessive or codominant. In the default codominant option, heterozygote selection is calculated by taking half of the reduction in movement probability that a homozygote with induced plasticity (state = ‘2,2’) would have, as defined by the user (see subsection ‘Habitat Selection Process’). Once induced, the state of the allele for plasticity remains until the end of the organism's life, representing irreversible plasticity. When mating, offspring inherit the genotypes using the existing CDMetaPOP Mendelian inheritance framework, but all inherited alleles are returned to the non-induced state, that is ‘2’ reverts to ‘1’ in offspring. If the ‘2’ was inherited, this would represent a form of transgenerational plasticity not yet implanted in the software. The plastic allele may also be representative of a polygenic region encompassing multiple loci, assuming high linkage where induction of the plastic response occurs in unison across linked loci.

2.3 | Habitat selection process

Movement in the plasticity module is a function of the environment experienced and the genotype of the individual. In summary, the steps of the module broadly involve two user-defined thresholds: (1) inherit alleles, (2) experience patches during life span while migrating to and from natal grounds, with a variety of patch-specific temperatures or habitat quality values encountered, (3) induce future habitat selection if the environment exceeds the first user-defined induction threshold, dependent on an individual having the plastic allele(s) (4) and, once induced, alter future dispersal probability based on the second user-defined habitat selection threshold, (5) pass alleles to offspring, but not induction state. The plasticity induction threshold determines temperature or habitat value which induces the plastic response. The second parameter is the habitat selection response threshold, which represents the temperature (or habitat quality) value that generates a behavioural response post-induction. In this case, a patch is avoided during migration by induced individuals if temperature exceeds the habitat selection threshold. Specifically, individuals in a given environment within a patch will become induced if the patch trait, either temperature or habitat quality, exceeds the user-defined threshold for triggering the response (see Figure 1 for diagram of overall CDMetaPOP framework and module order). The selection occurs during ‘Migrate back’ and ‘Migrate out’ steps because these represent the movement to breeding/natal patches and dispersal away from natal patches, respectively. Then, during all future movement processes, if an individual has the allele for the plastic response (a single or double copy depending on user inputs) and the allele(s) has been induced; then, those individuals have a lower probability of settling into patches with temperature or habitat values greater than or equal to the habitat selection value, which we refer to as the temperature avoidance threshold value. Notably, habitat selection thresholds are also user-defined and can differ from selection thresholds. For example, a user may scale habitat quality from 1 to 10 (with 1 being the best habitat), set the induction signal response threshold to 3 such that selection behaviour is induced if a patch with this value or greater is encountered, and a selection threshold of 8 whereby patches with habitat quality 8 or greater are avoided if an individual has the plastic allele and it has been previously induced. Thus, besides deciding on whether temperature or habitat quality should be used as the environmental factor for selection, users select the strength of response, and whether the response is dominant, recessive or codominant (e.g. see ‘Behavioral Plasticity Module’ section for more details). An example of the flow of the module is shown in Figure 2.

2.4 | Model expectations of the plasticity module under a simple temperature landscape

We assessed whether the new module met expectations by running a simulation on a hypothetical landscape with three patches: one below the induction and habitat selection temperature thresholds, one at the induction temperature threshold and one above the induction selection threshold that was also above the habitat selection temperature. This served as a quasi-validation or evaluation step (Augusiak et al., 2014). In this case, we expect to see lower population size in the patch with the avoidance temperature. We used inputs to establish panmixia to avoid any spatial structuring of the environment. If the module was operating correctly, induced individuals should avoid the patches where the temperature was above the avoidance threshold and individuals in patches above the induction threshold would have their plasticity switches turned on. To confirm that the thresholds were being implemented correctly, we also ran simulations where the induction and avoidance temperatures exceeded any of the patch temperatures, that is no habitat selection would be induced. We ran these models for 50 years, with a species with a 1-year generation time for a single replicate. In addition, we explored the sensitivity to the initial conditions. In addition, we explored the sensitivity of the initial conditions by running different proportions of individuals with the plastic allele (roughly 0.50–0.99) with the hypothetical population over 20 years.

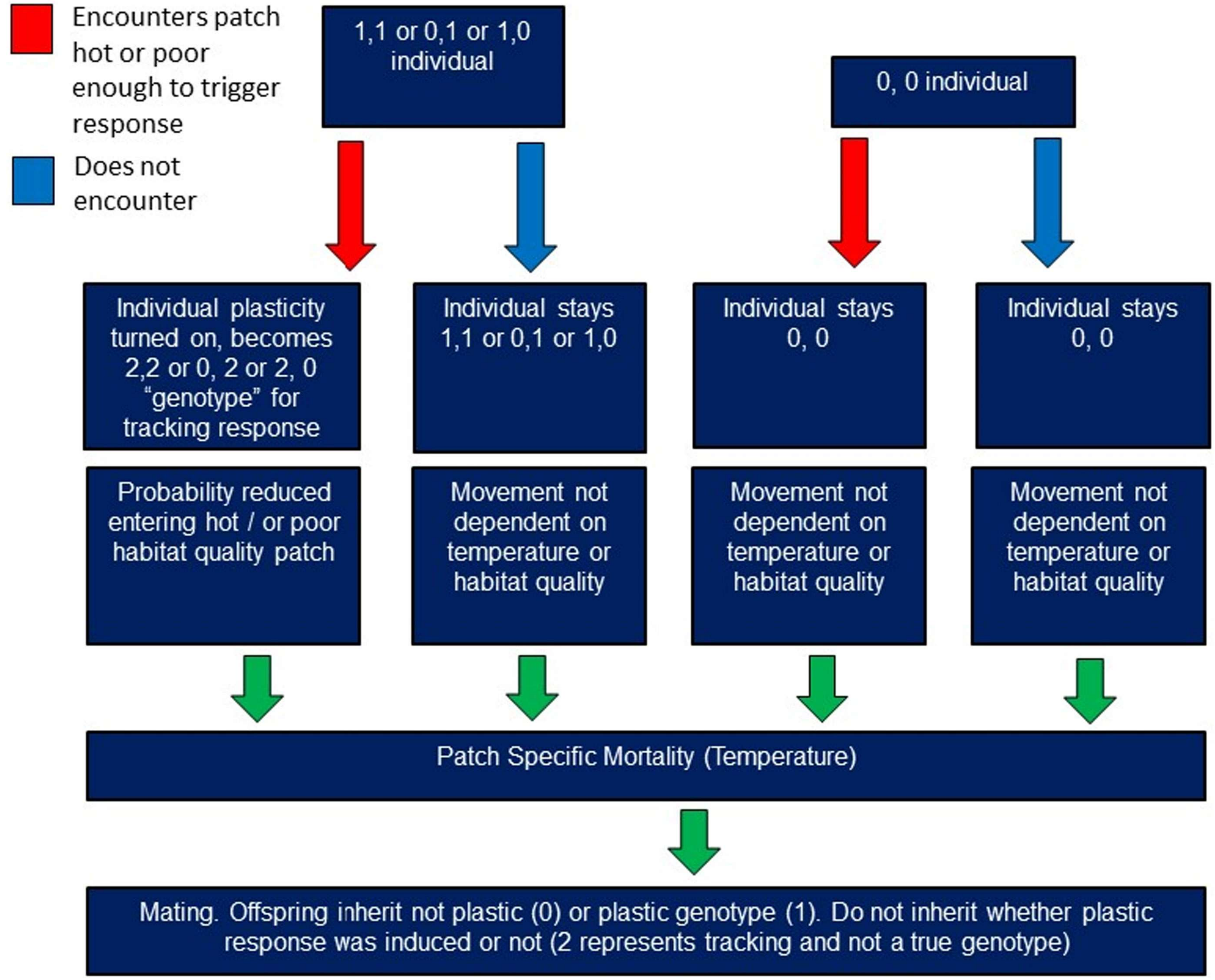


FIGURE 2 Conceptual framework for applying new module. User defines the trigger for induction of the response, as well as the environmental threshold to be avoided after induction. In the given example, the trigger will turn on the plastic response if the individual has the plastic allele ('1') and encounters temperatures greater than a user-defined value, and in response avoids all patches during migration with a temperature greater than a user-defined threshold. Trigger and response are set independently. Trigger and response may be based on the temperature or use defined habitat quality at a patch and may change through time. The individuals who encounter the plastic signal threshold are shifted to a new 'genotype' by changing their '1' alleles to '2', which is used for tracking the phenotypic response of adjusting movement on the landscape and does not represent a true genotype that is passed to offspring. Consequently, the induced state is not inherited, and instead only the '0' or '1' alleles.

2.5 | Empirical example simulations with the plasticity module

To illustrate the new module in an empirical system, we ran simulations of redband trout (*Oncorhynchus mykiss gairdneri*) in three watersheds across Idaho. The three stream networks represent a 'cool' montane system (Keithley and Mann creeks), a 'desert' system (Jacks Creeks) and an intermediate 'dry' stream with a gradient from cool montane conditions in upper reaches to intermittent drying events in lower reaches and overall higher habitat heterogeneity (Dry Creek). We selected these three stream networks due to the variety of temperature gradients between the streams and within the stream networks. To prepare the patch input file, we segmented the river into 100-m patches or reaches through each network. The number of patches for 'cool' was 1505, 'desert' was 2570, and 'dry' was 615. All patches were given an equal carrying capacity with a mean of 100 and a standard deviation of 10 with the density-dependent class-specific population model using a normal distribution. For movement and the probability of movement matrices, we calculated pairwise river distance using least-cost path estimates using the 'gdistance' package in R v4.0.2 (van Etten, 2017; R Core Team, 2020). Mean riverine distance was roughly 33.7, 11.7 and 10.0 km for the Jacks Creek System, Dry Creek and within the Keithley/Mann system (which are disjunct). For the temperatures during the spring/summer steps of the model, we used the estimated August temperatures from

NorWeST (Isaak et al., 2017). These models encompass the relative carbon pathway (RCP) 6.5, implemented in the years 2040 and 2080, as a stepwise function. Additional patch-specific mortality rate of 0.40 was implemented when temperatures were greater than 20.6°C, a threshold shown to be physiologically stressful for fish based on lab experiments on fish from Big Jacks Creek (Chen et al., 2018).

We ran simulations using projected stream temperature data through 2100 under four broad scenarios: warming climate with (1) an allele conferring thermal tolerance, (2) an allele for the plastic response to patch temperature using the new module, (3) both of these alleles, and (4) neither of these alleles and subsequent loci. The initial allele frequency of the plastic allele was set to be common (0.66) in the population to help demonstrate the proof of concept across many individuals avoiding the hot patches. Probability of maturation was set for each body size class, and generations were allowed to overlap. Each scenario was run for 10 replicates. For the locus conferring thermal tolerance, the temperature-dependent, patch-specific mortality rate was reduced to 0 for homozygotes with the adaptive allele and to 0.20 for heterozygotes for all temperatures above 20.6°C. The mortality occurred only during the spring/summer period of the year. The plasticity induction threshold was set to 16°C and the habitat selection threshold was set to 20°C, with a habitat selection probability of 0.0 for patches over 20°C (i.e., complete avoidance of hot patches by induced individuals). We used the most extreme avoidance level to highlight the whether the module was working as anticipated. Avoidance of a patch occurred for both heterozygotes and homozygotes of the plastic allele and occurred during both the migration out and back steps. We note that in this model of a salmonid fish, migration steps are separated from the probability of dispersal from the natal site to a breeding site ('straying') in the model; both movement properties are user defined. We tracked the thermal tolerance, thermal preference, and one neutral locus and its alleles, regardless of whether the natural selection or plasticity modules were turned on. This was done to confirm that the modules were not impacting the simulations when they were not anticipated to. Specifically, we anticipated lower abundance in the high-temperature patches when adding habitat selection given the strong habitat selection. In addition, we predicted that the rate of increase in the thermal tolerance allele would be slower when habitat selection was occurring because selection for the thermal tolerance allele would be weaker when individuals avoided patches with high thermal mortality. All input parameters can be found at https://github.com/trasea986/3_site_ABM.

Simulation output included the location and genotype of each individual every 10 years, as well as whether they were expressing habitat selection conferred by the plasticity module. Additional individual data are available from CDMetaPOP simulations, but we focused all analyses on these values. We tallied the number of individuals in each patch and calculated proportion of the thermal tolerance allele, the plastic allele and one neutral locus. The neutral locus allowed us to assess the potential role of genetic drift in the models. For example, a larger shift in neutral allele frequencies than thermal tolerance or plasticity alleles would indicate that drift was the most important factor in shifting allele frequencies.

3 | RESULTS

3.1 | Model expectations of the plasticity module under a simple temperature landscape

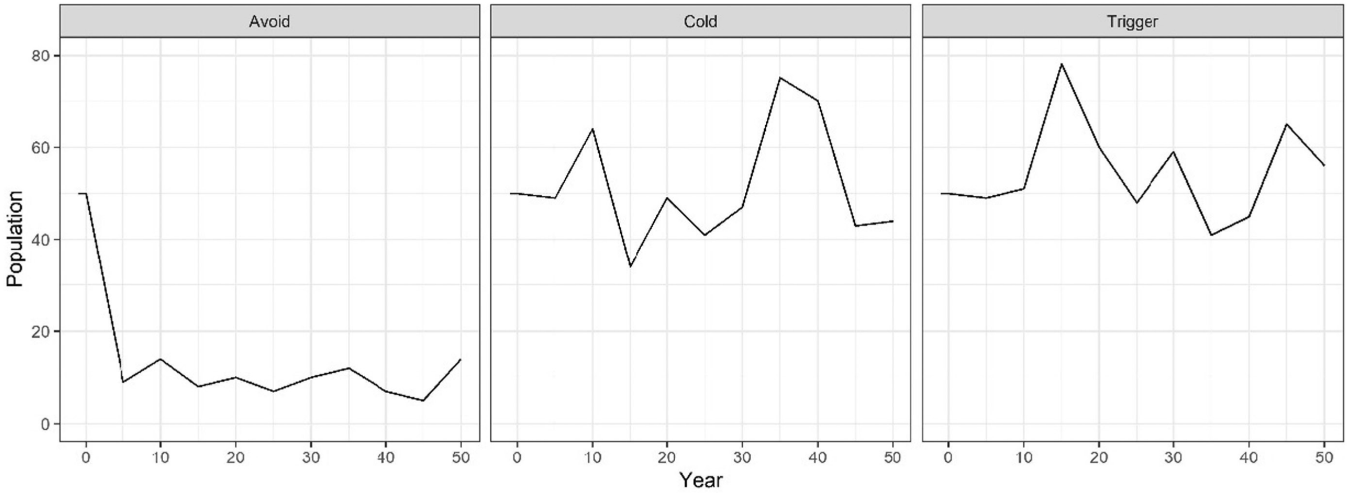
The first set of simulations enabled us to evaluate how the new module's spatially explicit functionality would affect resulting population responses. Overall occupancy of the patches matched expectations based on the model inputs. In the hypothetical landscape, individuals avoided the expected patches and the number of individuals occupying the patches above the avoided temperature threshold decreased through time (Figure 3a). This pattern disappeared once the plasticity module was shut off (Figure 3b). The hypothetical population was not sensitive to the initial starting proportion of individuals with the plastic allele (Figure S1). However, some systems may be sensitive to starting frequency of the plastic allele if, for example the strength of selection on traits (including plasticity) is very high or the system is prone to drift. The use of sensitivity tests by users will help elucidate emergent properties of their model system, and we encourage users to conduct their own sensitivity analysis for their input parameters.

3.2 | Model evaluations of the plasticity module with empirical examples

Occupancy of the patches also occurred as expected in the redband trout simulations example (Figure 4). In the empirical trout example, patches where temperatures exceeded 20.6°C were less likely to be occupied in the null model due to the high (40%) mortality rate in those patches compared with when the thermal tolerance allele was included in the model, and the difference was most apparent when comparing the cool montane stream network to the desert stream network (Figure 4). The networks also had the expected result of those patches remaining almost completely empty when the behavioural plasticity module was included (Figure 4). The lower (warmer) mainstem reaches of the Dry Creek system above the threshold were also avoided when the plasticity module was used (Figure S2). The effect became more obvious at the end of the climate warming scenario, when a larger proportion of patches exceeded the temperature threshold for both cool montane and desert networks. Including the thermal preference, plastic allele greatly changed occupancy. Although not biologically realistic that avoidance would be 100 percent, this setting allowed for quick identification of patches that are being avoided, and to confirm that module results were as anticipated.

One consequence of the shift in occupancy with the four model scenarios was a change in population dynamics with climate change

(a) Plasticity On



(b) Plasticity Off

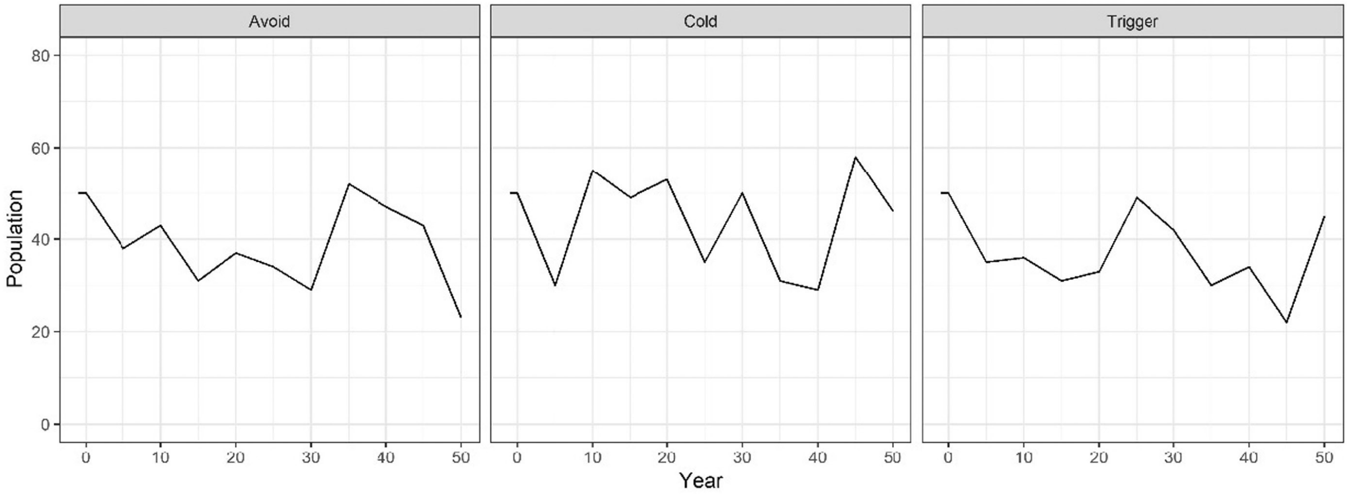


FIGURE 3 Population size occurring across a hypothetical landscape for proof of concept from 5 to 50 years, under a state of panmixia when plasticity temperature module was on (a) or off (b) with all other inputs remaining the same. To turn the module off in this case, we set the trigger and response temperatures to higher than the temperature of any of the patches. Listed temperatures/patch names for each of the three patches in the simulation are relative to user inputs, where the Trigger patch was where the plastic allele could be turned on, and where the 'Avoid' patch was avoided if individuals had the plastic allele and it was turned on. This Avoid patch would also turn on the allele if present. Output of simulation results was in 5-year increments.

(Figure 5). The presence of the allele for thermal tolerance increased the population size, but this was only clear in the desert system. By completely avoiding patches, which did not guarantee mortality in the model, the population sizes of the system were decreased in both the plasticity model and tolerance-plasticity model. Again, this was most apparent in the desert ecosystem compared with the others, where the number of patches exceeding the trigger threshold was the greatest. The decline is an implicit opportunity cost for those with the plastic allele—by never gambling on a warm patch after induction, they lost fitness on average.

Over the course of the simulations, we observed the expected changes to the allele frequencies for the thermal tolerance allele and the thermal preference plastic allele for the cool montane and desert systems (Figure 6, Figure S3 for Dry Creek). Both remained similar to the neutral locus in the null model, although the initialization step did have the plastic locus starting with initially high frequencies of the plastic allele, but not induced. There were some changes in the allele frequencies at the neutral locus, likely due to drift and population decline with climate change. The allele for thermal tolerance increased with time and did so at a faster rate in the desert system. Although the proportion of individuals without the plastic allele remained roughly the same, the proportion of individuals in an induced state increased through time in the cool and desert populations as anticipated with climate change and the overlapping generations of the simulated fish. Populations also plateaued as they approached equilibrium below the system's defined carrying capacity. When running both the selection and plasticity modules with the alleles for thermal tolerance and thermal preference, we saw a decline in the rate of spread of the thermal tolerance allele because avoidance of hot patches pre-empted selection for thermal tolerance. Thus, habitat selection functionally

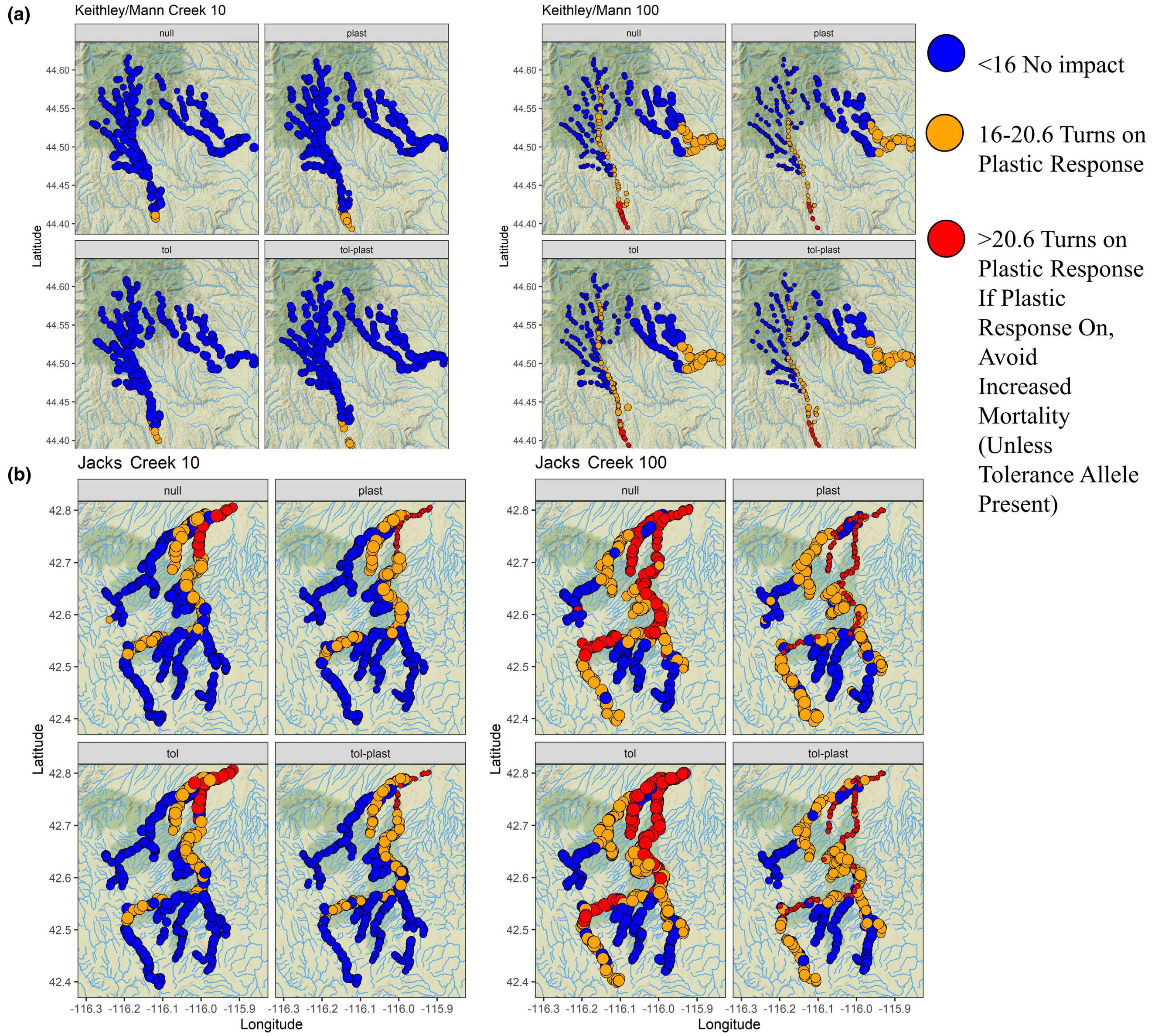


FIGURE 4 Result of the (a) cool montane and (b) desert stream networks for *O. mykiss gairdneri* at simulation year 10 and 100 with climate change based on NorWeST stream temperature models for August. The four models represent the presence of a thermal tolerance allele ('tol') which reduces mortality from 40 to 20 for heterozygotes and 0 for homozygotes; habitat selection for avoiding thermally stressful patches with a trigger temperature of 18°C and then total avoidance of 20°C ('plast'); or a combination of the two or neither ('tol-plast' and 'null', respectively). Size of circles for each patch represents the mean number of individuals present across 10 replicates, of all age classes, with red = patch avoided, yellow = patch triggers response and blue = cold patch below trigger threshold. 20% of patches were selected to show for clarity. Carrying capacity for the density-dependent, class-specific population model was set to 150,600 (cool; Keithley/Mann) and 257,000 (desert).

reduced network connectivity, and the reduction was most clear in the cool montane system, where the proportion of individuals with the thermal tolerance allele was less dynamic than the neutral alleles. Results were very consistent across replicates, except for at the cool montane sites, which had high variation in allele frequencies. Because of the variation in the neutral allele frequencies, drift likely is the dominant evolutionary process in the Keithley–Mann Creek system. This system was the smallest by size and carrying capacity, and was also the only site where the system included two disjunct stream segments, highlighting the potential importance of population size and network structure on simulation outcomes.

4 | DISCUSSION

Here, we present the first spatially explicit way to simulate inducible plasticity under the framework of habitat selection based on either thermal or habitat quality preferences that are tied to the individual genotype and environmental experience. Because of the ability to simulate individuals with or without the ability to have a plastic response, this module also allows for selection on behavioural or development plasticity to be explicitly simulated. By using an expansion to the existing CDMetaPOP framework, we also present the first software to allow simulation of multilocus selection and inducible

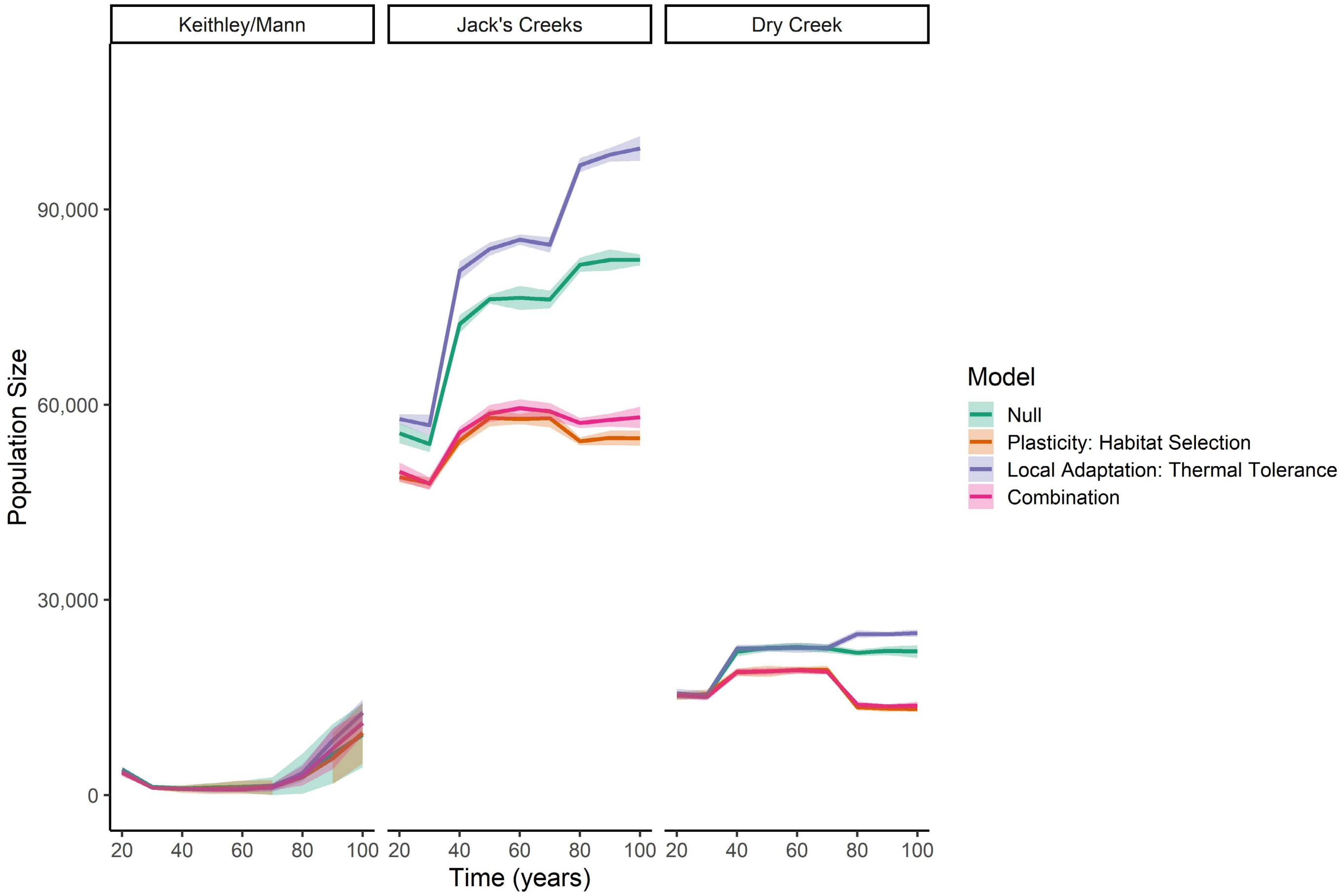
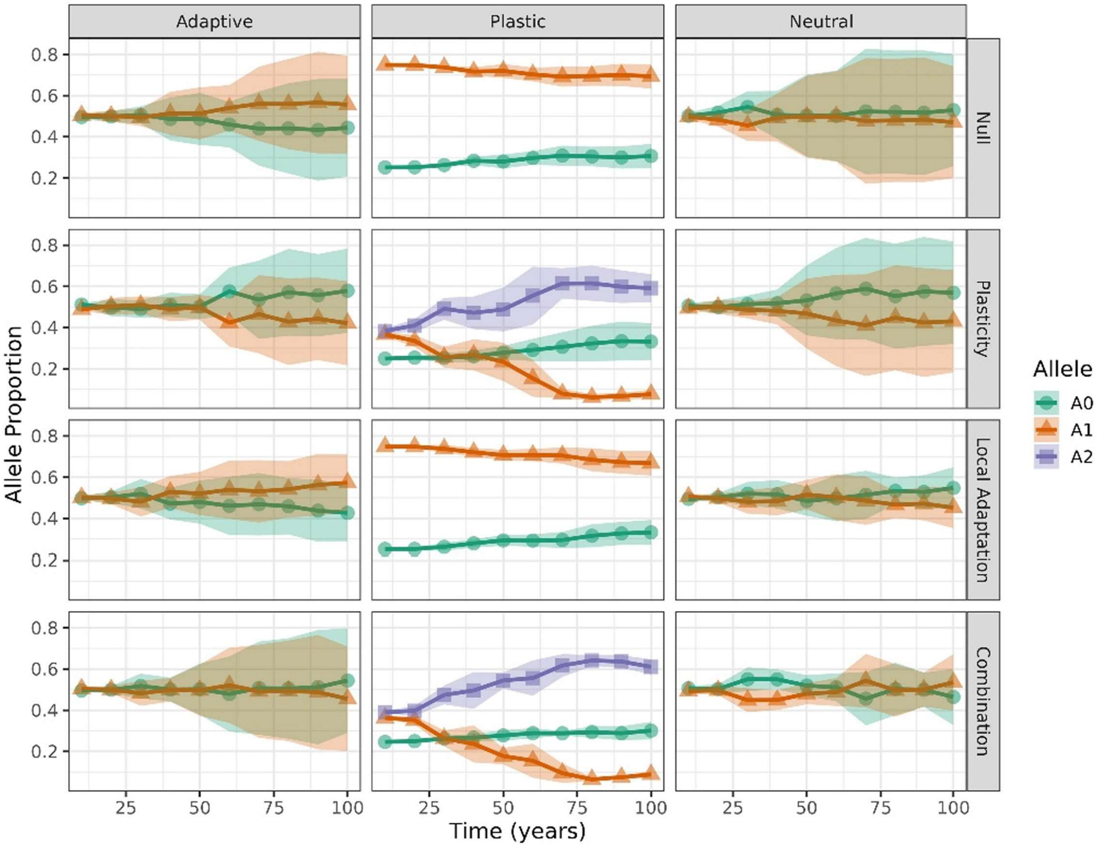


FIGURE 5 Number of individuals across cool montane and desert stream with climate change based on NorWeST stream temperature models for August. The four models represent the presence of a thermal tolerance allele ('Local Adaptation: Thermal Tolerance') which reduces mortality from 40 to 20 for heterozygotes and 0 for homozygotes; habitat selection for avoiding thermally stressful patches with a trigger temperature of 16°C and then total avoidance of 20°C ('Plasticity: Habitat Selection'); or a combination of the two or neither ('Combination' and 'Null', respectively). Carrying capacity for the density-dependent class-specific population model was set to 150,600, 257,000 and 61,500 for the cool, desert and dry scenarios, respectively. Shading represents standard deviation across the 10 replicates.

plasticity together to better understand the relative contributions of adaptive potential and plasticity to the persistence of populations in changing environments. Our redband trout simulations helped verify the module and simulated the effect of inducible behavioural avoidance on patch occupancy, population abundance and genetic composition in three representative populations. This expansion could apply to other species where the experience of a thermally stressful environment changes movement patterns (van Beest et al., 2012). Although there are other software options for population genetics that include some form of plasticity, the CDMetaPOP software allows users to simulate the actual evolution of plasticity while addressing behavioural plasticity explicitly. For example, SLiM can have fitness simulated independent of mutations (Haller & Messer, 2019) but, without additional coding, would not allow behavioural plasticity to then dictate the fitness function based on the landscape and simulated species. With RangeShifter, plasticity may be invoked for the emigration steps based on the explanation of the manual, and dispersal may evolve; however, plasticity is not directly tied to the spatially explicit, genotype-environment interaction (Bocedi et al., 2021). HexSim and other software lack reference and ability to work with plasticity (Schumaker & Brookes, 2018). Regardless, it is not surprising that the available programs as mentioned above for riverscape and landscape genetic simulations focus on different processes and represent environmental heterogeneity in different ways. As mentioned in Landguth et al. (2017), including the same biological processes across multiple software programs gives researchers the chance make inter-model comparisons. By addressing research questions using different software and models, additional information may be gained due to the different software and model assumptions (e.g. Blair et al., 2012; Landguth et al., 2017; Safner et al., 2011).

Our proof of concept empirical example provides an example of one of many research questions that may be addressed with this new module related to temperature. An expansion of our demonstration models with more robust empirical data would allow users to explore the relative importance of behavioural plasticity and thermal tolerance, as we begin to demonstrate here. In addition, researchers may be interested in questions related to how habitat selection may influence distributions and population dynamics, including scenarios with imperfect habitat selection. Pairing this

(a) Location cool



(b) Location desert

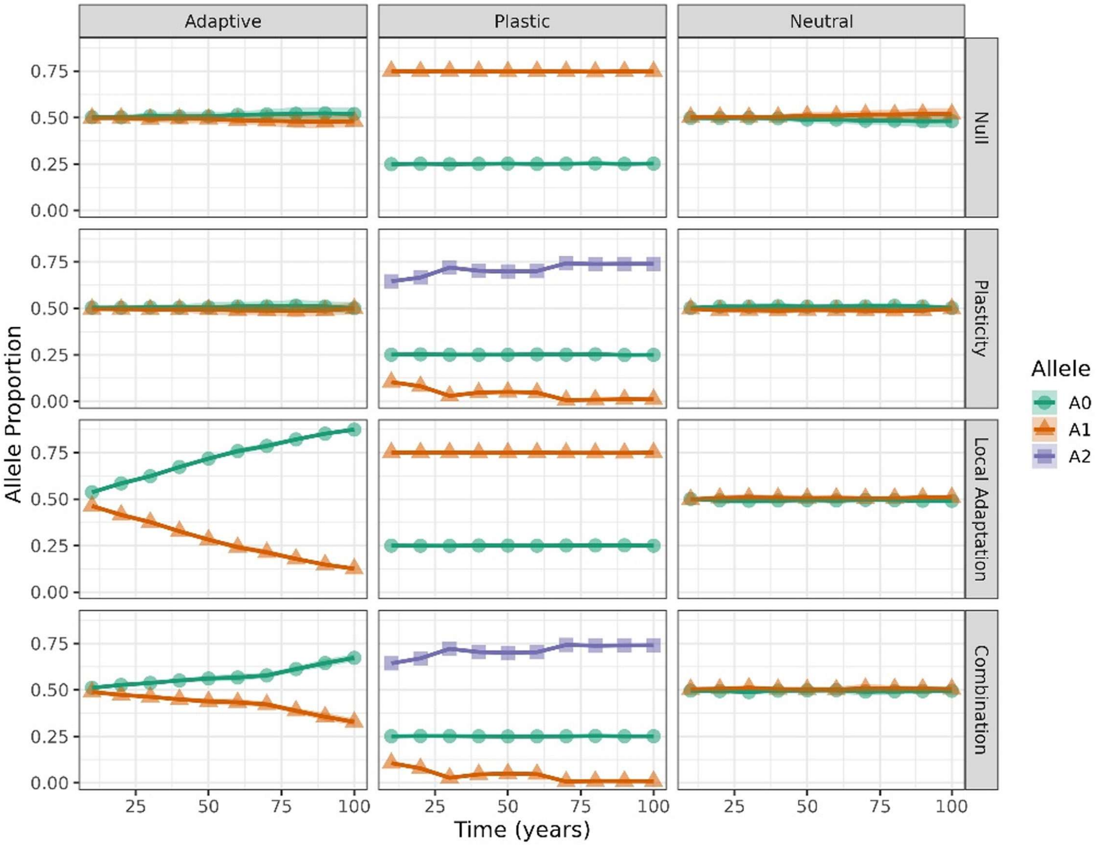


FIGURE 6 Allele proportions for (a) Keithley/Mann Creek and the (b) Jacks Creeks with climate change based on NorWeST stream temperature models for August. Loci A0 and A1 represent alleles 0 and 1 for the Adaptive (thermal tolerance) and Neutral loci, respectively. Allele 0 provides higher thermal tolerance at the adaptive locus. The plasticity region is different, with A0 for the plastic locus represents absence of the plastic allele, while A1 represents presence of the allele in the non-induced state and the induced state is represented by A2. A2 is used to track the induction state but does not represent a true allele that can be inherited. The four models represent the presence of a thermal tolerance allele, A0, ('Local Adaptation') which reduces mortality from 40 to 20 for heterozygotes and 0 for homozygotes; habitat selection for avoiding thermally stressful patches with a trigger temperature of 18°C and then total avoidance of 20°C ('Plasticity'); or a combination of the two or neither ('Combination' and 'null', respectively). Because of the selected parameters, habitat selection prevents individuals from entering patches below carrying capacity when in the induced state, but warm patches do not have complete mortality, resulting in an overall indirect cost to the plastic response. Shading represents standard deviation across 10 replicates.

new module with existing modules also opens many questions. For example, researchers may want to investigate the role that seasonal movements and thermal habitat selection may interact with the predation/harvest module. If researchers elect to use temperature-dependent growth, they could examine feedbacks among thermal preference, growth and average fecundity. Another available model is the ability to model two hybridizing species, so researchers may explore the role of habitat selection and hybridization dynamics. Beyond these applications, researchers may be interested in using the software to help with study design for sampling schemes when habitat selection may be an important ecological component of their research.

This module presents users with flexibility for simulating plasticity and habitat selection beyond the presented examples for thermal tolerance. The permanent induction in the CDMetatPOP model reported here is somewhat unrealistic for modelling habitat selection behaviours in the trout ABMs presented because behaviours are often reversible. However, we note many plastic traits are constitutive (e.g. inducible defences to specific predators in *Daphnia*, Weiss, 2019) and some behavioural decisions are fixed after exposure to an environmental cue. For example, some behaviour traits and many morphological traits can be irreversible with predator exposure (Dahl & Peckarsky, 2003; Peckarsky, 1996; Weiss, 2019), which could be modelled by using the habitat quality plasticity options if the distribution of the predators are known. Although we selected temperature thresholds on the landscape for turning the plastic allele 'on', users may select a threshold below any value on the landscape, so that all individuals exhibit habitat selection. For example, past hydraulic or foraging experiences alter habitat selection (Capra et al., 2017; Stamps & Davis, 2006), so researchers may choose to simulate changes in the foraging environment due to anthropogenic changes. In addition, we presented example simulations for a thermal tolerance allele and thermal preference with our selection of using the temperature option for the simulation. Users may additionally select to use the habitat quality patch variable, and this would allow for habitat selection for a landscape variable other than temperature, while still evaluating the impacts of the thermally adapted alleles if using the multilocus selection module. For example, quality could be set to correlate with important habitat factors, such as the presence of cover or pool depth for trout (Dieterman et al., 2018), density, predators or to account for social dominance hierarchies. While we simulated the effect of an inducible behaviour on distribution, the module could simulate the role of social interactions related to density or territoriality within patches during the dispersal and patch selection processes by setting the habitat quality of the patch to correlate with these other patch features. Numerous studies have found that density or territoriality influence dispersal or habitat selection (Lutz et al., 2015; Muller et al., 1997; O'Neil et al., 2020; Stamps, 1991). In addition, the described habitat quality triggers and responses could be inverted in the input files and used to investigate maladaptive habitat selection (e.g. Hale & Swearer, 2017).

Even with limited simulations, we found interesting patterns across the *O. mykiss* populations. Habitat selection may likely have positive or negative impacts depending on the flexibility of habitat selection, and the cost of selecting poor habitat. There is a long history of exploring the impacts of habitat selection on population dynamics, generally linked to source–sink dynamics (Iii, 2003; Pulliam & Danielson, 1991), and it is encouraging to see the presence or absence of habitat selection create large shifts in the population dynamics of species in a changing environment. In particular, it was counterintuitive that a highly selective plastic response reducing individual mortality through thermal exposure resulted in lower population size. This result implies an indirect fitness cost of plasticity; however, it is important to note that the models are currently linked to assumptions that need to be assessed through continued empirical work, in this case the relationship between local density and thermal habitat selection behaviour. This mimics the ideal despotic distribution where habitat selection keeps individuals out of some patches and drops the overall population abundance, which has been observed in other trout species (Purchase & Hutchings, 2011). The drop in abundance was because we constrained the system such that the ideal free distribution could not be achieved. In contrast, the simulations with natural selection only are more similar to the ideal free distribution, although the assumption of perfect knowledge or the ability to access all patches means these simulations still stray from the ideal free distribution expectations (Kacelnik et al., 1992). These results also add to the general body of literature on whether plasticity may enhance or slow adaptive evolution, which in some cases has found that plasticity and adaptive evolution occur in opposite directions (Ghalambor et al., 2015). Whether plasticity facilitates or impedes adaptive evolution is related to whether plasticity may move traits close to new trait optimum values (Ghalambor et al., 2007).

Additional simulations will help to elucidate the relationship of thermal tolerance and preference, and how these two traits will play a role in the adaptive capacity of the species. As a better understanding of thermal tolerance, local adaptation, thermal preference and site-specific demographics emerges, we will be refining models to use this empirical data. The current habitat selection module caused binary habitat selection choices and deviations from the ideal free distribution, likely because the strong avoidance (1.0) was not balanced against the mortality risk (0.4 in non-thermally adapted individuals) of selecting a hot patch in summer. Future modelling effort could examine the evolution of the selection effect by allowing a selection threshold to evolve (i.e. as a norm of reaction threshold). It should be noted that one of the locations had much higher variation in simulations than the other three, and in that case, genetic drift, as measured by the allele frequencies of the neutral locus that was simulated, shifted as much as the tolerance and plasticity alleles. Thus, future work should continue to evaluate both neutral and adaptive alleles to assess the relative roles of selection and drift on modelled dynamics.

Future plans include multiple additions to t module. Firstly, costs may limit plasticity in habitat selection or other plastic traits (Edelaar et al., 2017; Scheiner et al., 2020), but cost is not directly applied in this model outside the indirect cost of avoiding potential patches. Secondly, the induction was irreversible, but future versions will include a decay function representing return to a base behavioural state after a threshold stimulus representing, for example weakening of habitat selection behaviours in induced individuals during later life history stages. In some systems, reversible behaviour may be more appropriate. This is likely if the behavioural response is linked to developmental and/or morphological plasticity (West-Eberhard, 2005). Time spent in a stressful environment is also an important part of whether the plastic response would be reversible (Gabriel, 2005). In the case of our models, with two seasonal steps each year, individuals are dealing with long exposure times relative to their overall lifetime, with our module aligning with plasticity related to mitigating current and future stress (Smallegange, 2022). In our simulations, reversible plasticity would dampen all effects observed for habitat selection including the observed reduced population sizes. While we chose to initially model irreversible plasticity because this was more tractable, reversible responses are common as noted above and thus future module expansions will need to account for the spectrum of reversible to irreversible plasticity. Thirdly, by resetting to the non-induced state after each breeding step we are not capturing potential inter-generational induction through maternal effects or epigenetic changes, which may induce changes in behavioural traits in offspring (Ledón-Rettig et al., 2013; Rey et al., 2020). Allowing transmission of the status of the plastic trait across generations would increase the impacts of the plastic response, which would also result in the proportion of individuals with the plastic response having a time lag to any changes in the environment. The current module is set up only for a single locus. With multilocus selection to CDMetaPOP already present (Landguth et al., 2020), we hope to also expand the module to and habitat selection model to also be an additive function across multiple loci to, for example facilitate modelling of the evolution of plasticity itself by allowing variance in thresholds and linking threshold values to individual loci (i.e. modelling norms of reaction).

5 | CONCLUSIONS

This module represents the first modelling framework for a genetically based form of phenotypic plasticity (GxE), which can also be simulated simultaneously with natural selection on genetic traits (G) in a spatially explicit and individual-based manner. This expansion will allow for both applied and basic biological questions. For example, theoretical landscapes could be implemented with CDMetaPOP to investigate how the spatial configuration of landscapes or temporal heterogeneity (e.g. press vs. pulse disturbances) affect the evolution of plasticity. For applied questions, these models could be used for evaluating alternative environmental scenarios and management actions at local scales (e.g. riparian management or management of thermal refuges) while accounting for varying degrees of habitat selection. Simulating individuals in models with sufficiently realistic eco-evolutionary traits (including plasticity) in these applied projects is critical to identify system attributes, both environmental and social, that will increase the adaptive capacity of systems in the face of changing environments and climate.

AUTHOR CONTRIBUTIONS

T. S. performed all analyses and wrote the manuscript with guidance from the authors. E. L. and T. S. worked on the coding for the new module. All authors were involved in experimental design, writing and editing.

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DATA AVAILABILITY STATEMENT

All simulation input files and processing scripts are available at https://github.com/trasea986/3_site_ABM. CDMetaPOP and user manual are available at https://github.com/ComputationalEcologyLab/CDMetaPOP.

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SUPPORTING INFORMATION

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