

## A spatially-explicit, individual-based demogenetic simulation framework for evaluating hybridization dynamics

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### ABSTRACT

Spatially-explicit individual-based simulation models provide a valuable tool for exploring complex ecological and evolutionary processes that are not easily empirically measured. Here, we present modifications of a spatially-explicit individual-based simulation model (CDMetaPOP) to accommodate a two-species system and simulations involving interspecific hybridization. We first describe how a hybrid (H) index is used to distinguish individuals of interspecific descent from those of either parental species. User-defined thresholds provide flexibility in the degree of admixture tolerated for classifying 'pure' individuals. We then detail relationships further informed by the H index, including individual growth, temperature-based fitness and selection, and mate preference behavior. Empirically derived species- and system-specific information can be incorporated into these relationships, for example, to produce differential growth among hybrids and parental species. Lastly, we demonstrate an application of this simulation framework by exploring the relative effects of temperature-based selection, mate preference behavior, and hybrid fitness on the rate and spatial extent of sympatric hybridization between two native riverine fish species, bull trout (*Salvelinus confluentus*) and Dolly Varden (*Salvelinus malma*), in the upper Skagit River system (United States and Canada). Results from this demonstration provide guidance for future empirical studies of bull trout, a federally threatened species. Understanding factors that contribute to the initiation and maintenance of hybridization, as well as the ecological and evolutionary consequences of this phenomenon, is of increasing importance given shifting species ranges due to large-scale landscape modification and a changing global climate. Our framework can be used to study a wide range of hybridization dynamics in any terrestrial or aquatic system, including comparisons of distinct environmental conditions or potential management responses.

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## 1. Introduction

Anthropogenically-influenced hybridization between closely related native species, or between native and introduced species, can result in irreversible ecological and evolutionary (eco-evolutionary) consequences that pose a significant threat to biodiversity worldwide (Rhymer and Simberloff, 1996; Todesco et al., 2016). These consequences range from genetic homogenization (McKinney and Lockwood, 1999; Olden et al., 2004) to parental reinforcement (Servedio and Noor, 2003; Mallet, 2005), and in extreme cases, local or global extinction of native species can occur (Levin et al., 1996; Todesco et al., 2016). Spatial distributions of species are increasingly altered by processes including large-scale landscape modification and global climate change, providing new opportunities for hybridization between previously isolated species. Effective mitigation of such hybridization threats requires a better understanding of factors influencing hybridization dynamics (Allendorf et al., 2001; Seehausen et al., 2008; Hoffmann and Sgrò, 2011).

Evolutionary processes, demographic characteristics, and landscape features collectively influence hybridization dynamics among species, but the interactive effects of these factors on the initiation, persistence, and outcomes of hybridization are poorly understood. Identifying mechanisms underlying these processes, and their relative influence, will not only improve our understanding of the evolutionary role of hybridization (e.g. Barton, 2001), but also provide practical guidance for mitigating negative impacts on native species (Wood et al., 2015; Samson et al., 2017; Boyd et al., 2018). For example, understanding the relative fitness of hybrids under distinct environmental conditions can provide insights into the expected rate and extent of adaptive introgression (Barrett and Schluter, 2008; Hedrick, 2013), and the likely spatiotemporal stability of a hybrid zone (Buggs, 2007; Taylor et al., 2015). However, empirical assessment of both the drivers and consequences of interspecific hybridization is often impracticable, and in such instances complex eco-evolutionary relationships may best be explored through simulation.

In recent years, spatially-explicit individual-based models (IBMs) have become valuable tools for simulating dynamic eco-evolutionary relationships due to the increasing ability of these models to represent detailed demographic and genetic (demogenetic) processes (DeAngelis and Grimm, 2014). IBMs can account for inter-individual variation (i.e., age, size, maturity) essential for understanding complex relationships across ecological scales (DeAngelis and Gross, 1992; Grimm, 1999; DeAngelis and Mooij, 2005). Simulations of interspecific hybridization under contemporary and future conditions can help improve our theoretical understanding of the drivers and consequences of hybridization (McLane et al., 2011; Grimm et al., 2017). Additionally, IBMs can be parameterized to facilitate empirical evaluations that provide practical guidance for conservation and management. Recent studies have demonstrated eco-evolutionary applications of IBMs in terrestrial and aquatic systems (Frank et al., 2011; Munroe et al., 2012; Landguth et al., 2014, 2017a; Selkoe et al., 2016). However, the utility of these models in improving our understanding of mechanisms contributing to interspecific hybridization and in predicting the fate of evolutionary lineages remains largely unexplored, in part due to the inability of IBMs to incorporate multiple species-specific parameterizations in heterogeneous landscapes (but see Della Croce et al., 2014).

Here, we extend a previously existing, spatially-explicit demogenetic IBM (CDMetaPOP; Landguth et al., 2017b) to provide a framework for evaluating hybridization dynamics between two species. We first describe the use of a hybrid (H) index (Campton and Utter, 1985; Buerkle, 2005) to distinguish individuals of interspecific descent from those of either parental species. We then detail relationships further informed by the H index, including individual growth, temperature-based fitness and selection, and mate preference behavior. We also discuss how species- and system-specific information can be used to apply this framework to a broad range of taxa and ecological systems,

and the use of sensitivity analyses to guide future research in systems with high uncertainty. Finally, we demonstrate an application of our framework by evaluating sympatric hybridization dynamics for two native riverine fish species, bull trout (*Salvelinus confluentus*) and Dolly Varden (*Salvelinus malma*), in a portion of the Skagit River extending through Washington (United States) and lower British Columbia (Canada). The Skagit River serves as one of a few population strongholds for bull trout (United States Fish and Wildlife Service, 2015), a species listed as threatened in the United States and of special concern in Canada (COSEWIC, 2010; United States Fish and Wildlife Service, 2015). Sympatric hybridization between bull trout and Dolly Varden was recently genetically confirmed in some portions of the Skagit River (Small et al., 2015), therefore posing a concern for bull trout conservation in this region. Mechanisms facilitating hybridization between bull trout and Dolly Varden are presently unknown, and simulations provide a valuable approach for guiding future empirical research efforts.

Specific objectives of this study were to: (1) implement an H index relationship in CDMetaPOP to facilitate the distinction of individuals representing two parental species and their hybrids, (2) extend biological and demographic parameters in CDMetaPOP to accommodate species-specific values, and (3) demonstrate an application of the modified CDMetaPOP framework by exploring the relative influence of temperature-based selection, mate preference behavior, and hybrid fitness on the abundance and spatial distribution of bull trout-Dolly Varden hybrids in the Skagit River.

## 2. Methods

### 2.1. Simulation model

Briefly, CDMetaPOP is a landscape-level, individual-based, demogenetic model of meta-population processes. These processes are simulated as interactions among individuals located across a number of spatially explicit ‘patches’ comprising meta-populations. Each patch is designated as either a natal (i.e., spawning) or migratory (i.e., over wintering, non-spawning) patch. Individuals within a patch are assumed to share a common environment (e.g., carrying capacity, temperature). Within each patch, a length- and age-based class structure is used to simulate complex stochastic demogenetic processes, while movement of individuals (i.e., migration, straying) among patches occurs as a function of spatially-explicit landscape permeability surfaces (Appendices 1, 2, and 3). At the patch level, individuals undergo growth, reproduction, migration, and mortality, and resulting demographic and genetic processes are simulated over time at the individual level. Below, we highlight novel relationships implemented in CDMetaPOP (v1.10) as part of our framework for evaluating hybridization dynamics. Detailed descriptions of processes simulated by CDMetaPOP can be found in Landguth et al. (2017b), the user manual (<https://github.com/ComputationalEcologyLab/CDMetaPOP>), and online appendices of this manuscript.

### 2.2. Modification of CDMetaPOP to evaluate hybridization dynamics

Modifications to the existing CDMetaPOP framework included implementation of an H index to represent individual-based admixture, modification of input file capabilities to allow the specification of biological parameters for two parental species, and incorporation of biological relationships informed by H index. The H index-informed biological relationships are used to specify individual growth, temperature-based selection and fitness, and mate preference behavior. Each of these relationships are described in detail below.

#### 2.2.1. Identification of parental species and hybrids

An H index was used to reflect the genetic composition of individuals, and to distinguish individuals of either pure parental species from those of interspecific descent. Genotypes for the two parental

species are assigned values at opposite ends of a bounded numerical spectrum such that the H index for all individuals range from zero to one. Within the model, users can specify minimum and maximum admixture thresholds for distinguishing “parental” species. Some applications may prefer strict cutoffs of  $0 < \text{H index} < 1$  to distinguish hybrids from pure parental species, though defining ecologically appropriate admixture thresholds for conservation purposes can be challenging and context-specific (Allendorf et al., 2001). We therefore implemented the H index relationship in a manner that allows users flexibility in the specification of admixture thresholds.

Eggs are assigned an H index intermediate to the H indices of the parents. Parental H indices are also used to assign class characteristics (e.g., age and size class, migration and stray probabilities) to offspring (Appendix 1: Table S1); this assignment is based on a weighted random draw such that an individual with H index  $< 0.50$  is more likely to be assigned the class characteristics of parental species A, and an individual with H index  $> 0.50$  is more likely to be assigned the class characteristics of parental species B. Individual H indices are then used to specify species-specific demographic parameters such as growth, fitness, and mate preferences.

### 2.2.2. Individual growth

Individual growth in CDMetaPOP is divided between two user-specified time steps: spawning and non-spawning. We implemented a new module (‘temperature and statistical fitting for growth with H index’; see CDMetaPOP user manual) for controlling growth based on the H index and class characteristics of an individual. This module uses spatially-explicit temperature values at each patch to determine growth for each individual, and requires three user-specified elements: von Bertalanffy growth parameters (von Bertalanffy, 1938), a temperature-growth response curve, and the number of days during which individuals are exposed to patch-specific temperatures for growth (see CDMetaPOP user manual). We used a linear relationship (Eq. (1)) to modify the  $L_{\infty}$  parameter and incorporate the H index of an individual:

$$L_{\infty}' = (\text{H index}) * (L_{\infty B} - L_{\infty A}) + L_{\infty A}, \quad (1)$$

where  $L_{\infty A}$  and  $L_{\infty B}$  correspond with the  $L_{\infty}$  for individuals of parental species A (lower H index) and parental species B (higher H index), respectively.

### 2.2.3. Temperature-based selection and fitness

We modified the CDMetaPOP framework to enable temperature-based selection through two processes: (1) parental species thermal tolerances, wherein we assumed that optimal fitness coincided with user-specified species-specific temperature optima, and (2) hybrid fitness relative to either parental species. We used the H index of a given individual to identify the optimal temperature for that individual. We then implemented a linear relationship to associate individual H index with the mean of species-specific Gaussian distributions centered at the temperature optima specified for parental species A and B. The degree of overlap in the range of fitness values for parental species A and B was controlled by the standard deviation parameter of the Gaussian distribution, where a smaller standard deviation results in a narrower fitness range and stronger selection. A hybrid fitness parameter was used to control the fitness of hybrids relative to either parental species. Thus, overall fitness was defined by a Gaussian function of natal patch temperature and by the H index of an individual as described in Eq. (2):

$$\text{Fitness} = p * \exp(-X_j - (\text{mintemp} + (\text{maxtemp} - \text{mintemp}) * \text{H index})^2 / (2 * C^2)), \quad (2)$$

where  $p$  is the fitness of hybrids relative to parental species,  $X$  is the temperature at patch  $j$ ,  $\text{mintemp}$  is the optimal temperature of the parental species associated with the lower temperature optimum,  $\text{maxtemp}$  is the optimal temperature of the parental species associated with a higher temperature optimum, and  $C$  is the standard deviation

controlling the degree of overlap between parental species fitness values. Values for  $\text{mintemp}$  and  $\text{maxtemp}$  represent empirically determined temperatures corresponding with optimal body growth in each parental species.

### 2.2.4. Reproduction and mate preference behavior

Three distinct mate preference behaviors are now possible in the modified CDMetaPOP mate module which allows users to explore a wide range of dual-species applications. In all cases, mate selection operates by females selecting a male within the spatial range specified by the mating cost distance matrix (Appendix 3). One mate preference behavior option implements random mating wherein there is no mate preference between species (hereafter “random mating”). A second option restricts mating to intraspecific pairs, where mates must be of the same parental species in order to mate (hereafter “intraspecific mating”). This second option has a strict threshold as distinguished by individual H indices (see Section 2.2.1) that only allows mating to occur between pairs of the same species. Hybrids will therefore not occur and this scenario would only be useful for null models or other non-hybridization based questions. A third option facilitates mating such that individuals prefer (but are not restricted to) mates of the same species (hereafter “self-preference mating”). In the third option, the degree of mate preference ( $\phi_{i,j}$ ) is determined using a linear model (M'Gonigle and FitzJohn, 2010) modified to incorporate the H indices of each potential mate pair as described in Eq. (3):

$$\phi_{i,j} = (1 + (1 - \text{abs}((\text{female H index}) - (\text{male H index}))) * (\text{assortative mate factor} - 1)) * f_j, \quad (3)$$

where  $f_j$  denotes the frequency of H indices binned at intervals of 0.10 in the patch of the female. The *assortative mate factor* determines the strength of assortative mating and ranges from one to infinity, where a larger value corresponds with stronger self-preference. Under this linear-preference assortative mating model, mate selection occurs with a higher probability given greater similarity of H indices between a female and potential mate. However, hybridization is still possible with high *assortative mate factor* values if no optimal mate pair exists within a given patch (see discussion); this mate preference behavior option therefore does not restrict mating to intraspecific mate pairs. Importantly, regardless of the mate preference behavior implemented in a simulation scenario, mating is primarily restricted to individuals present within the female’s patch at the onset of the mating module.

### 2.3. Demonstration of hybridization framework

To demonstrate an application of the CDMetaPOP modifications described above, we evaluated hybridization dynamics between two native salmonids, bull trout (BT) and Dolly Varden (DV), in the upper Skagit River. Specifically, we used our simulation framework to explore the effects of temperature-based selection, mate preference behavior, and hybrid fitness on the spatiotemporal abundance and distribution of BT-DV hybrids (Table 1). This application of our framework required the parameterization of several relationships to describe inter- and intraspecific demogenetic processes; these parameters are described in Appendices 1, 2, and 3.

We expected our simulation framework to show greater spatial overlap between mature BT and DV in tributaries where water temperatures were intermediate to temperature optima for both species, and in instances where temperature-based selection was weak. However, spatial overlap does not necessarily result in interbreeding (Robbins et al., 2014), and we also evaluated the effect of distinct mate preference behaviors. We anticipated that reduced preference for mates of the same species would increase the rate of hybridization. Finally, hybrid fitness is a strong determinant of short- and long-term impacts of hybridization, including the fate of either parental species (Burke and Arnold, 2001; Seehausen, 2004). The relative fitness of BT-DV hybrids

**Table 1**

Description of simulation scenarios evaluated in this study. The variables (mate preference behavior, temperature-based selection, hybrid fitness) implemented in each scenario are provided, as well as the setting for each variable. Values of NA indicate that the associated variable was not implemented in the simulation scenario.

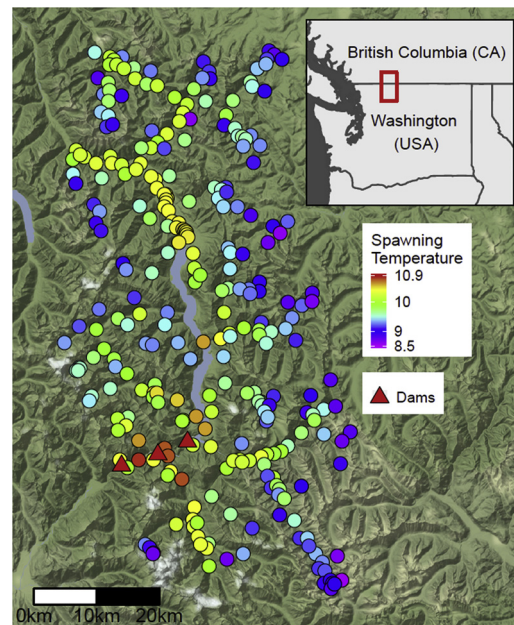
Mate Preference Behavior	Temperature-based Selection	Hybrid Fitness
Intraspecific	NA	NA
Intraspecific	Low	NA
Intraspecific	High	NA
Random	NA	NA
Random	Low	100
Random	High	100
Random	Low	75
Random	High	75
Random	Low	50
Random	High	50
Self-preference	NA	NA
Self-preference	Low	100
Self-preference	High	100
Self-preference	Low	75
Self-preference	High	75
Self-preference	Low	50
Self-preference	High	50

has not been empirically studied, so we used a range of values to evaluate model sensitivity to the fitness parameter (Table 1). We evaluated simulation scenarios with and without a hybrid fitness penalty, and expected that reduced hybrid fitness would result in a decreased rate of hybridization, and increased persistence of parental species. Though the anticipated outcomes of our hypotheses appear intuitive, exploring contemporaneous interactions of these variables (temperature-based selection, mate preference behavior, and hybrid fitness) in the context of a heterogeneous environment provides a worthwhile investigation of the relative effect of each factor on the dynamics of hybridizing species.

### 2.3.1. Study system and temperature model

The spatial extent of our study system was constrained to a segment of the upper Skagit River north of Gorge Dam and extending from Washington (United States) to lower British Columbia (Canada; Fig. 1). This extent contained 286 patch locations spatially-delineated based on stream segment catchment areas defined using ArcHydro Tools 10.2 (ESRI, Redlands, California). Three dammed reservoirs were included in the study system (Gorge Lake, Diablo Lake, and Ross Lake; Fig. 1). Downstream migrations of bull trout through these dams are rarely observed (E. Connor, *personal observation*), and dams were therefore considered complete barriers to movement for the purposes of this demonstration. Patches were designated as either natal ( $n = 275$ , mean area = 4.11 ha [0.04–28.77]) or non-spawning ( $n = 11$ , mean area = 743.66 ha [0.49–4734.82]) habitats based on stream temperature, and modified based on available biological information. Both BT and DV were allowed to spawn in each natal patch; however, the spatial distribution of both species was influenced by temperature-based selection. Patch carrying capacity was determined by habitat area in each patch, with a density of one individual per 100 m<sup>2</sup> of stream surface area; this density is consistent with that observed in surveys of tributaries in the upper Skagit River (E. Connor, *unpublished data*) and is also within the range of other values reported from the region (McPhail and Baxter, 1996). Stream surface area was calculated for each patch as the product of stream segment length and estimated bankfull width, inferred using Pacific Northwest regional hydraulic geometry equations developed by Castro and Jackson (2001).

Given a lack of in situ temperature data for the full extent of our study system, we predicted stream temperature from air temperature using the methodology described in Arismendi et al. (2014). Air temperature is often used as a proxy for stream temperature when in situ



**Fig. 1.** Map of the upper Skagit River system used for demogenetic simulations. Patch centroids (circles;  $n = 286$ ) and patch stream temperatures (color scale) are shown, as well as the location of three dams within the study system (triangles). Temperatures (°C) were averaged across the spawning time period specified in this demonstration (August 1 - October 15) using air temperature data sourced from Worldclim BioClim.

temperature data are unavailable and prohibit the use of other methods (Stefan and Preud'homme, 1993). Mean monthly air temperature was calculated as the average of 30 Arc second maximum and minimum air temperature data from Worldclim BioClim (Hijmans et al., 2005); detailed data required for the calculation of median monthly air temperature are not available through this database. Predicted stream temperature was averaged across the months included in the two time periods specified in our model, spawning (August 1 - October 15; Fig. 1) and non-spawning (October 16 - July 31; Appendix 4: Fig. S2).

### 2.3.2. Species-specific parameters

We designated parental species A (H index = 0.0 - 0.1) as DV and parental species B (H index = 0.9–1.0) as BT. We chose admixture thresholds (0.1 - 0.9) based on those commonly used to identify hybrids with genetic data (Vähä and Primmer, 2006; Harbicht et al., 2014) and values used to classify salmonid populations for conservation purposes (e.g. Shepard et al., 2005). Values for species-specific parameters were based on empirically determined values (Appendix 1: Table S1), but supplemented with information from local experts when empirical values were lacking. Briefly, we initialized the model at time = 0 with a random distribution of individuals characterized by an equal sex ratio and comprising eight age classes (ages 0–7) for each parental species. Each age class was assigned a species-specific mean length and standard deviation (Appendix 1: Table S1; Triton Environmental Consultants, 2008; Bowerman, 2013; Mims et al., 2019). Size-linked parameters vary as individuals grow and enter subsequent size classes. For both BT and DV, the probability of migration increased with size, with a maximum probability of 0.572 associated with the largest size classes (Appendix 1: Table S1; Mims et al., 2019). Due to unknown straying rates for BT and DV, a stray probability of 0.01 was used for all size classes for both species. Relationships describing individual maturity and fecundity were informed by individual length and therefore differed between species (Appendices 1 and 2). We used an independent mortality of 60% to determine survival of eggs to fingerlings (Mims et al., 2019).

To inform temperature-based relationships for growth, fitness, and selection, we used optimal temperatures of 10.5 °C and 8.5 °C for BT

and DV, respectively (Appendix 1: Table S1; Appendix 5: Fig. S3). This optimal temperature value is lower than those reported in laboratory studies of bull trout (13 °C, Selong et al., 2001; 16 °C, Mesa et al., 2013), but similar to those reported in an empirical study of bull trout in the upper Skagit River (10.9–15.4 °C, Eckmann et al., 2016). Furthermore, Dunham et al. (2003) reported maximum densities of juvenile bull trout in streams with maximum temperatures of approximately 10 °C. The optimal temperatures specified for BT and DV in this study also fit the range of temperatures observed in our stream temperature model, and reflect the colder waters preferred by DV relative to BT.

To inform the growth of BT and DV, we used parameters from von Bertalanffy (Bowerman, 2013) and temperature-growth (Selong et al., 2001) relationships previously developed for BT, except  $L_{\infty}$  was derived from empirical observations of BT and DV in the upper Skagit River system (E. Connor, unpublished data). In Skagit River populations of BT and DV, adult BT are considerably larger than adult DV and may reach lengths of 700 mm and 300 mm, respectively, with hybrid individuals reaching intermediate sizes (E. Connor, unpublished data). For the growth model described in Eq. 1, differential sizes of BT, DV, and hybrid individuals were achieved by scaling  $L_{\infty}$  to an individual's H index while using the same temperature-growth response curve for both parental species. In reality, the growth of an individual is likely influenced by the biologically inherent  $L_{\infty}$  of a species as well as ambient temperatures. Thus, our Skagit-specific values of  $L_{\infty}$  used for BT and DV and the stream temperatures used in our study combine to achieve individual sizes that match empirical observations. This strategy provides a direct mechanism for creating differential growth between our study species, and is suitable for a modelling framework designed to explore interspecific hybridization in a variety of systems.

### 2.3.3. Simulation scenarios

We performed model sensitivity analysis by conducting a factorial design simulation experiment to explore how variation in temperature-based selection, mate preference behavior, and hybrid fitness affect the rate and spatial extent of hybridization, and abundance of hybrid and parental individuals (Table 1). We evaluated two temperature-based selection scenarios wherein selection strength was either low ( $C = 1.5$ ; Eq. (2)) or high ( $C = 1.0$ ). We also evaluated three mate preference behaviors: (1) random mating wherein no mate preference occurs, (2) intraspecific mating wherein mating is only possible within species, and (3) self-preference wherein individuals strongly prefer, but are not restricted to, mates of the same species. For scenarios with self-preference mating behavior, we set the assortative mate factor to  $10^{10}$  to produce strong mate preference. With this parameterization and given an even proportion of BT and DV in a patch, the probability of a female selecting a mate of the same species was  $> 99.9\%$ . Finally, we explored hybrid fitness relative to either parental species using three hybrid fitness levels: 100% (i.e. no fitness penalty), 75%, and 50%.

We assessed 17 distinct scenarios (Table 1), with ten independent Monte Carlo replicates for each scenario, resulting in 170 total simulations. The first scenario in Table 1 represents the null model evaluated in this study, wherein temperature-based selection was not implemented and interspecific hybridization was not allowed. This null model provided a baseline for comparison to all other scenarios in which different combinations of temperature-based selection and various mate behaviors were implemented. Each simulation scenario was run for a total of 280 iterations (hereafter referred to as years), representing approximately 56 generations of BT and DV based on an average generation time of five years (Scott and Crossman, 1973; Rieman and McIntyre, 1993; Rieman and Allendorf, 2001; COSEWIC, 2010). The first 50 years of a simulation comprised a population dynamics burn-in to stabilize age distributions. The temperature-based selection regime was implemented at year 50 following demographic stabilization, and mate preference behavior and hybrid fitness regimes were implemented at year 80 when models again reached stabilization; simulations then continued for an additional 200 years. The timing and

description of processes that occur within a single iteration of the model are shown in Appendix 1: Fig. S1. All simulations were performed on a Dell Linux cluster with CentOS 6.3 operating system (16x Quad-core 2.5 GHz processors with 512 GB RAM) at the University of Connecticut's Computational Biology Core facility.

### 2.3.4. Analysis of simulation outputs

Several individual-based and summary statistics can be output from CDMetaPOP, including statistics that describe both demographic and genetic relationships (see CDMetaPOP user manual). We used two methods to analyze simulation results from individual-based comma separated outputs. First, species counts were summed across all patches at ten-year intervals over the duration of the simulation. For simplification of output visualizations, we only present counts of parental and hybrid individuals ( $0.1 < H \text{ index} < 0.9$ ) averaged over ten Monte Carlo replicates, though individual H indices could also be used to evaluate the degree of admixture over the same population (e.g. F1-hybrid vs. F2-backcross). Second, patches containing both species were summed in each year to determine the degree of spatial overlap between BT and DV across our scenarios. For both analyses, we determined statistical significance based on confidence intervals calculated using  $mean \pm 1.96 * standard \ error$ , and plotted figures in R version 3.2.3 (R Development Core Team, 2017).

## 3. Results

### 3.1. Model development

We successfully integrated novel relationships into the existing CDMetaPOP framework that now facilitate multi-species parameterizations for the study of hybridization dynamics (Fig. 2). The overall workflow of this new framework (Appendix 1: Fig. S1) proceeds similarly to the original implementation of CDMetaPOP. However, species-specific relationships for individual growth, environmental fitness and selection, and mate preference are now possible based on the use of an H index to represent the degree of individual admixture (Fig. 2). Implementation of an H index allows hybridization to be spatiotemporally evaluated across a study system. In our demonstration of these new capabilities, varying species-specific parameters resulted in unique demographic outcomes and spatial distributions at multiple time points, illustrating that our framework can be used to assess the impact of evolutionary processes, demographic characteristics, and landscape features on hybridization dynamics.

### 3.2. Demonstration of hybridization framework

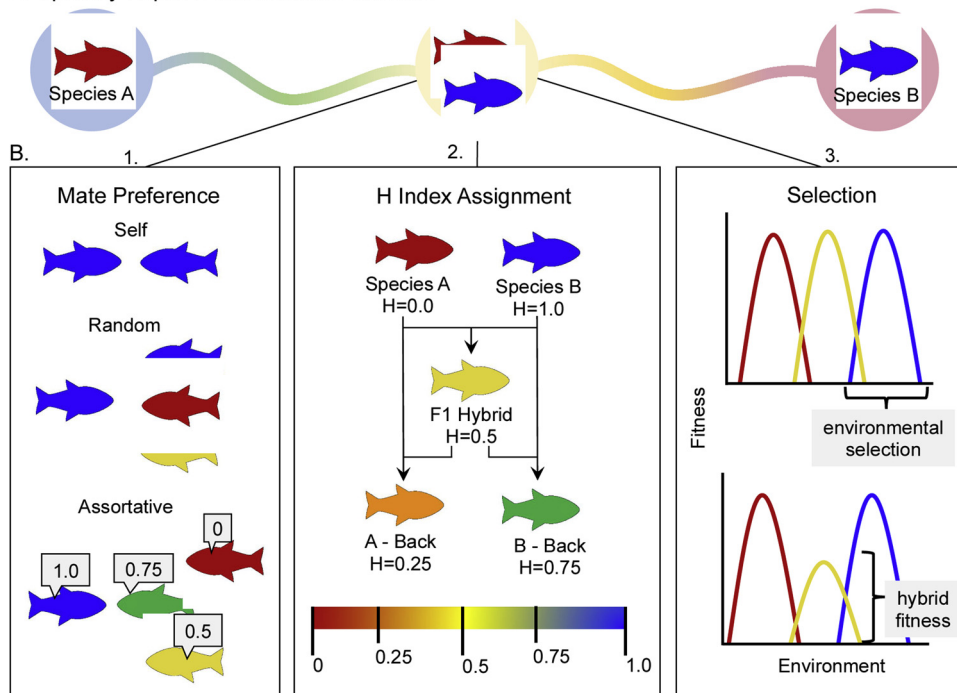
#### 3.2.1. Null model

Our null model was characterized by intraspecific mating and a lack of temperature-based selection, and resulted in a system with slightly higher abundance of DV relative to BT (mean DV = 31,150 [28,185–34,115] individuals; mean BT = 23,240 [22,329–24,152] individuals; Fig. 3a). This outcome likely resulted from the smaller body size of DV and the size-based patch packing algorithm implemented in CDMetaPOP (see CDMetaPOP user manual). Both BT and DV were randomly distributed across the study system due to a lack of temperature-based selection (results not shown).

#### 3.2.2. Temperature-based selection

Temperature-based selection affected the initial spatial distribution of BT and DV, in which patches hybridization initially occurred, and the rate at which hybrids dominated the system. In scenarios with intraspecific mating, the strength of temperature-based selection (high or low) determined the extent of spatial overlap between BT and DV. Across simulation scenarios, DV were primarily distributed in head-water tributaries of the study system and BT were primarily distributed in downstream river segments by the end of the simulated time period

## A. Spatially-Explicit Environmental Gradient



**Fig. 2.** Hybridization processes newly implemented in CDMetaPOP. Simulations are initiated with two species in a spatially-explicit environmental gradient in which species are spatially separated by environmental preference (A). In patches where the two species overlap following migration, the degree of interspecies mating is determined by mate preference behavior (B1), and resulting offspring are assigned an appropriate H index (B2). Individual fitness is determined by resident patch environment (B3, top) and H index (B3, bottom), as specified by the user.

(Appendix 6: Fig. S4). An average of 58.50 patches (SE = 9.22; 20.56% of patches) contained both species in the low selection scenario, and an average of 9.9 patches (SE = 2.79; 3.46% of patches) contained both species in the high selection scenario. Similarly, temperature-based selection influenced the initial spatial distribution of hybrids and parental species (Appendix 7: Fig. S5). In scenarios with high temperature-based selection, hybrids primarily initiated in headwaters of the system (Appendix 8: Fig. S6). In comparison, hybrids initiated in patches throughout the system in scenarios with low temperature-based selection. Temperature also influenced the rate at which hybrids appeared in the system. For example, in scenarios with random mating and intermediate hybrid fitness, approximately three times more hybrids were present at year 150 in the low temperature-based selection scenario (mean = 30,015 [22,320–37,709] individuals) relative to the high temperature-based selection scenario (mean = 8,725 [4,490–12,961] individuals; Fig. 4C and 4D).

### 3.2.3. Mate preference behavior

With the exception of the intraspecific mating scenario, mate preference behavior did not have a strong effect on the abundance of hybrids (Figs. 3–5). Scenarios with medium or high hybrid fitness and either random or self-preference mating all resulted in systems dominated by hybrids at the end of the simulated time period at a similar rate (Fig. 4 and 5). Mate preference behavior also did not influence the initial locations or the final spatial distributions of hybrids; results from scenarios with self-preference mating were similar to those for scenarios with random mating.

### 3.2.4. Hybrid fitness

Of the three parameters evaluated in this demonstration, hybrid fitness had the greatest influence on the abundance of hybrids present at the end of simulations. Reduced hybrid fitness resulted in an overall decreased abundance of hybrids and increased abundance of both parental species (Figs. 4 and 5). This trend was consistent across scenarios incorporating varying degrees of temperature-based selection and mate preference behaviors. In simulation scenarios characterized by random mating and low temperature-based selection, the number of patches containing BT increased from 6.2 (SE = 2.16; 2.2% of patches)

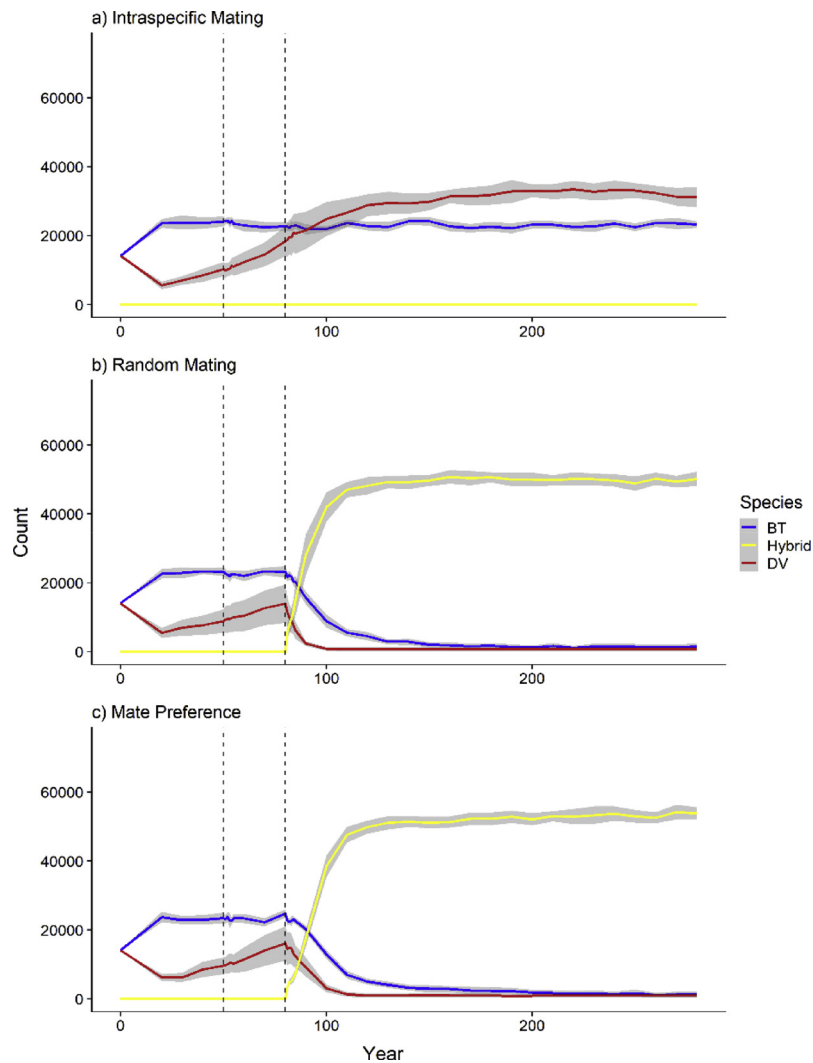
to 58.7 (SE = 16.52; 20.5% of patches) to 200.8 (SE = 3.77; 70.0% of patches), and the number of patches containing DV changed from 0.4 (SE = 0.4; 0.1% of patches) to 0.3 (SE = 0.3; 0.1% of patches) to 11.4 (SE = 5.64; 4.0% of patches), for scenarios with hybrid fitness equal to 100%, 75%, or 50% of parental fitness, respectively (Fig. 6).

## 4. Discussion

### 4.1. Framework for evaluating hybridization dynamics

We successfully extended a previously existing demogenetic simulation model (CDMetaPOP; Landguth et al., 2017b) to provide a framework for evaluating hybridization dynamics between two species. Specifically, we added capabilities for: (1) distinguishing parental and hybrid individuals based on degree of individual admixture, (2) producing species-specific and individual-based growth, (3) implementing species-specific and individual-based temperature-related selection, including the option for an individual-based fitness penalty, and (4) generating distinct mate preference behaviors. Species- and system-specific information can be incorporated into this framework to enable its application to any ecological system.

Though other IBMs have been developed for simulating hybridization dynamics, to our knowledge our framework is the first to incorporate detailed (i.e. more realistic) landscape and demographic features. Early IBMs for evaluating hybridization implemented one-dimensional grid systems (e.g. Cain et al., 1999) and were limited in their ability to represent complex spatial and demographic features. Sadedin and Littlejohn (2003) developed an IBM for evaluating species reinforcement that allows users to vary characteristics such as hybrid disadvantage and mate preference behavior. However, this IBM comprises individuals dispersed across a simple two-dimensional grid and does not account for spatial heterogeneity in landscape features and individual movement, nor does it incorporate population- or species-specific demographic characteristics, among other limitations. These limitations also correspond with an IBM developed by Thibert-Plante and Hendry (2009) to assess hybridization dynamics in the context of ecological speciation. More recently, Della Croce et al. (2014) developed an IBM to assess hybridization between riverine species; however,



**Fig. 3.** Species counts for the three model scenarios with no temperature-based selection and varying levels of mate preference behavior: a) intraspecific, b) random, and c) self-preference. Counts are summed across all 286 patches for 280 years of simulation. The vertical dashed line at year 50 indicates the end of the demographic burn-in (i.e., temperature-based selection begins), and the vertical dashed line at year 80 indicates the beginning of hybridization in the simulation model. Horizontal lines and shaded regions represent means and 95% confidence intervals based on ten Monte Carlo replicates. BT = bull trout; DV = Dolly Varden.

this model does not incorporate relationships for species-specific biological characteristics, and riverscape heterogeneity is restricted to variation in simple stream network topologies.

#### 4.2. BT-DV hybridization in the Skagit River

In the demonstration of our hybridization framework, we observed several relationships between bull trout and Dolly Varden that could help guide future empirical evaluations of these species. In particular, we found that temperature-based selection greatly influenced the initiation of hybridization. The distributional range of bull trout is largely parapatric with Dolly Varden (*Salvelinus malma*); however, a number of contact zones where these species occur in sympatry have been identified (Cavender, 1978; Haas and McPhail, 1991; McPhail and Taylor, 1995; Leary and Allendorf, 1997; Taylor et al., 2001). Hybridization between bull trout and Dolly Varden in areas of sympatry has been genetically confirmed for a number of these contact zones (Baxter et al., 1997; Taylor et al., 2001), though the rate of hybridization varies among watersheds (Taylor et al., 2001). Previous studies of species biology and ecology suggest that hybridization between bull trout and Dolly Varden may be more likely when size-dependent differences in spawning behavior and habitat choice are less pronounced (McPhail

and Taylor, 1995; Hagen, 2000; Dunham et al., 2008). For example, in regions where Dolly Varden and bull trout occur in sympatry, Dolly Varden typically use spawning habitat characterized by cooler water temperatures relative to bull trout (Hagen and Taylor, 2001); however, hybridization is possible in tributaries where the thermal regime facilitates the presence of both species.

Our simulations also demonstrated that the number of hybrids present at the end of simulations was most strongly affected by hybrid fitness. Empirical studies of temperature-based selection and the relative fitness of hybrids are currently lacking for bull trout and Dolly Varden, but results from studies of other salmonids demonstrate the importance of hybrid fitness to the long-term persistence of parental species. Ostberg et al. (2004) observed that hybrids of sympatric coastal rainbow trout (*Oncorhynchus mykiss irideus*) and coastal cutthroat trout (*O. clarki clarki*) display reduced fitness in parental habitats, facilitating the maintenance of parental species. In comparison, even low levels of admixture in westslope cutthroat trout (*O. clarkia lewisii*) due to hybridization with invasive rainbow trout (*O. mykiss*) correspond with marked reductions in reproductive success (Muhlfeld et al., 2009). Empirical studies of hybrid fitness, and the stability of this relationship across environmental gradients, would significantly improve our understanding of the impacts of sympatric hybridization on the

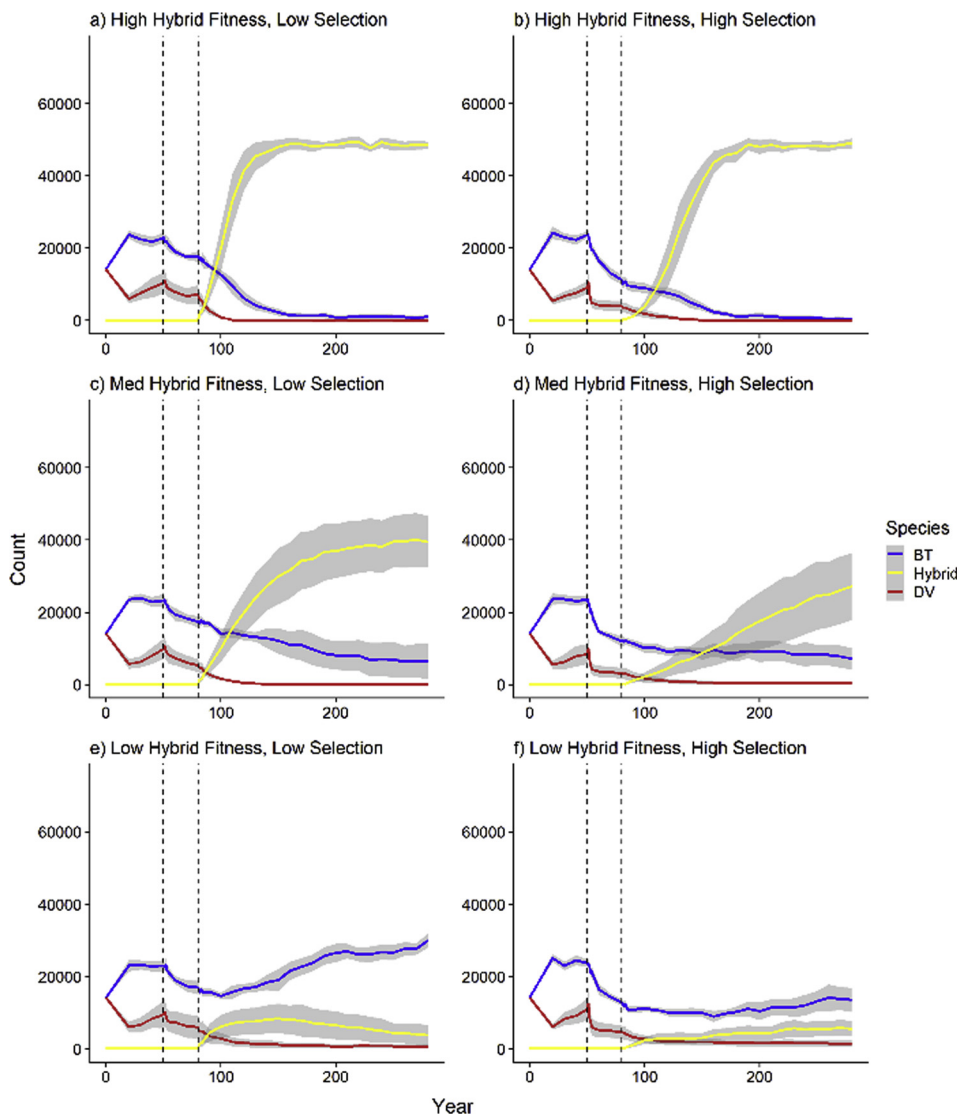


Fig. 4. Species counts for the six model scenarios characterized by random mating and varying levels of temperature-based selection (low: a, c, e; high: b, d, f) and hybrid fitness (high: a, b; medium: c, d; low: e, f). Counts are summed across all 286 patches for 280 years of simulation. The vertical dashed line at year 50 indicates the end of the demographic burn-in (i.e., temperature-based selection begins) and the vertical dashed line at year 80 indicates the beginning of hybridization in the simulation model. Horizontal lines and shaded regions represent means and 95% confidence intervals based on ten Monte Carlo replicates. BT = bull trout; DV = Dolly Varden.

evolutionary trajectories of bull trout and Dolly Varden in the Skagit River. Such studies are essential given that the Skagit River serves as one of a small number of population strongholds for bull trout (United States Fish and Wildlife Service, 2015), and resulting information could directly inform management and conservation policies.

Although we were able to draw from a moderate body of literature to populate our simulation model, empirical data were not available for every parameter. Future users of CDMetaPOP may be faced with similar challenges when focusing on less-studied species. In our demonstration, we showed how simulations can be used to evaluate relative sensitivity to model parameterizations in instances where empirical values are lacking. However, model validation can be challenging and often not feasible due to the large spatial scale and complexity of demographic and genetic processes. Hypothesis-based comparisons of competing model scenarios may be possible in cases where extensive empirical data exist, for example by using additional approaches to estimate parameters (e.g. Approximate Bayesian Computation [ABC]; Beaumont et al., 2002) in comparison to simulation outputs. In the case of our application, minimal empirical data were available for validating model outputs. Hybridization was only recently documented between bull trout and Dolly Varden in the Skagit River system (Small et al., 2015) and little biological information is known about the hybrid individuals. However, as demonstrated by our example application, simulations can still be a useful tool for identifying patterns to guide future empirical

studies, and to assist resource managers in the prioritization of conservation goals.

#### 4.3. Conservation applications

Our simulation framework can be easily adapted to explore hybridization dynamics in any heterogeneous ecological system. In particular, evaluating the relative importance of hybrid fitness across systems would provide additional insights into the broader biological significance of this relationship. For example, whether ecological segregation is a factor influencing hybridization dynamics for invasive rainbow trout and native westslope cutthroat trout has recently been the subject of considerable debate (Kovach et al., 2017; Young et al., 2017). Parameterization of our simulation framework with available species- and system-specific information would provide the opportunity to determine the relative effects of habitat preference, physiological differences, landscape variables, and other factors influencing the complex interspecific hybridization dynamics in fish (Scribner et al., 2001) or other taxonomic groups (see Mallet, 2005 and references within).

The influence of climate change on hybridization dynamics is of particular concern for long term conservation purposes (Muhlfeld et al., 2014, 2017). The modelling framework presented here is useful for exploring the effects of altered environmental conditions, such as



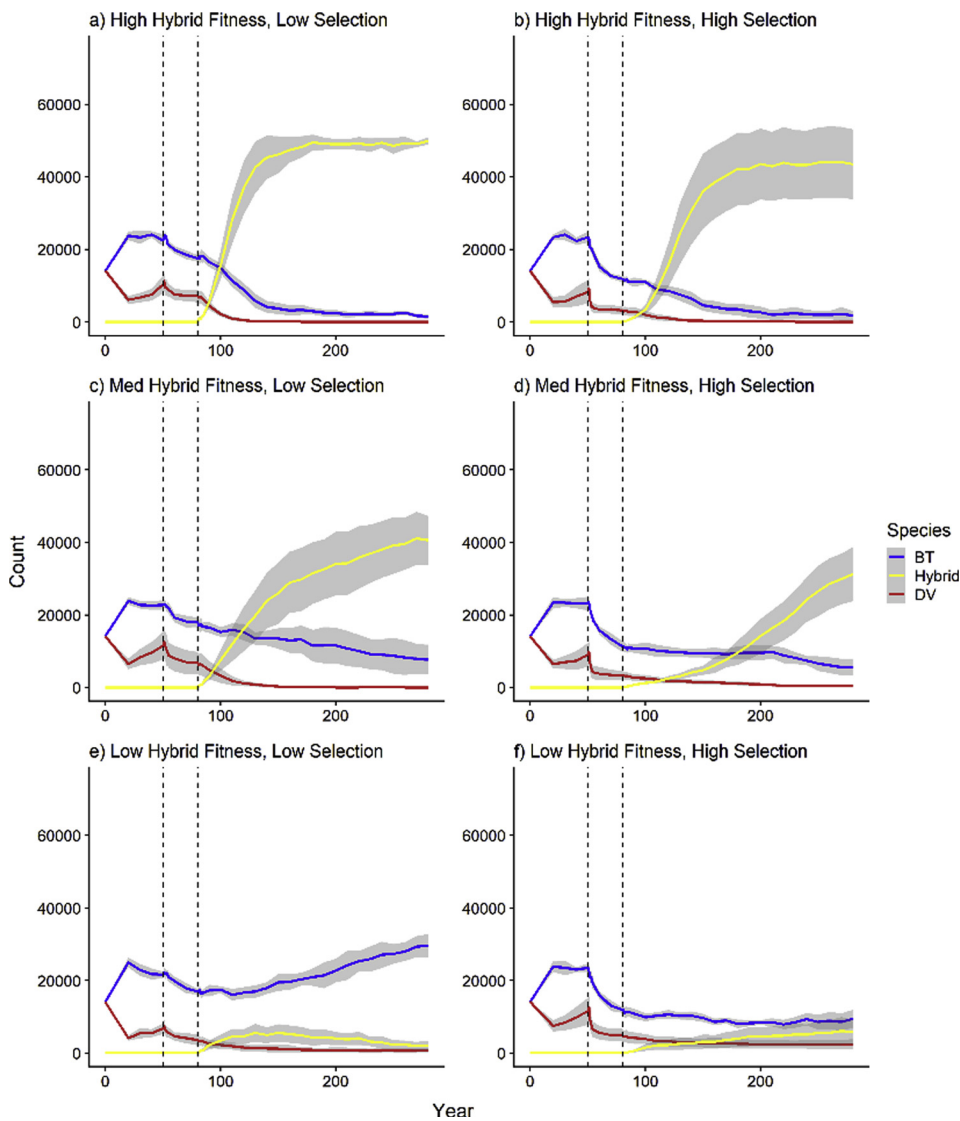


Fig. 5. Species counts for the six model scenarios with self-preference mating behavior and varying levels of temperature-based selection (low: a, c, e; high: b, d, f) and hybrid fitness (high: a, b; medium: c, d; high: e, f), summed across all 286 patches for 280 years of simulation. The vertical dashed line at year 50 indicates the end of the demographic burn-in (i.e., temperature-based selection begins) and the vertical dashed line at year 80 indicates the beginning of hybridization in the simulation model. Horizontal lines and shaded regions represent means and 95% confidence intervals based on ten Monte Carlo replicates. BT = bull trout; DV = Dolly Varden.

increased average temperature as a result of global climate change, on hybridization dynamics. Particularly for cold water lotic systems, which are likely to experience heterogeneous responses to a changing climate due to spatially distributed groundwater fluxes (Snyder et al., 2015), applications of IBM frameworks could help forecast future effects of climate change. For sympatric bull trout and Dolly Varden, such an investigation may initially result in increased spatial partitioning of species-specific spawning habitat, but an increase in temperature beyond the thermal tolerance of either species could have serious long-term consequences for these cold water fishes. Similarly, our modelling framework does not presently account for the capacity of parental species to adapt to such selective pressures. Studies on the possible evolutionary responses of salmonid species to climate change are challenging due to the difficulty of distinguishing between plastic and genetic-based phenotypic traits, and determining whether an observed phenotypic change is a direct adaptive response to climate change (Crozier et al., 2008; Merilä and Hendry, 2014). A small number of empirical studies suggest that salmonids have some potential to adapt to an altered thermal regime (Jensen et al., 2008). Modification of our simulation framework to evaluate adaptive capacity (Funk et al., 2018) would provide a valuable means for exploring the potential effects of climate change on hybridization dynamics in freshwater systems.

Other potential applications of our simulation framework center on predicting the effects of a broad range of management and conservation

actions. For example, our demonstration identified spatial areas especially prone to the development of interspecific contact zones; these zones could be targeted for monitoring to prevent interactions between parental species. Such applications are particularly useful for species that have a conservation emphasis, such as the critically endangered red wolf (*Canis rufus*), which is known to hybridize with coyotes (*C. latrans*; Bohling et al., 2016). Additionally, our simulation framework could be used to predict the effect of barrier implementation or removal on dynamics between potentially or currently hybridizing species to inform targeted management decisions (e.g. Novinger and Rahel, 2003). The effects of local land use practices can also be simulated by varying environmental variables, such as water flow or deforestation. Additionally, our framework can be used to explore the consequences of genetic rescue in inbred populations (Frankham, 2015; Whiteley et al., 2015), or to investigate the outcomes of recently debated actions such as intentional hybridization to promote climate adaptation (Hamilton and Miller, 2016; Kovach et al., 2016).

#### 4.4. Model limitations

A necessary future area of research is determining the biological relevance of the H index thresholds used in this study to distinguish hybrids from individuals of either parental species. Admixture thresholds appropriate for wild populations is a persistent and challenging

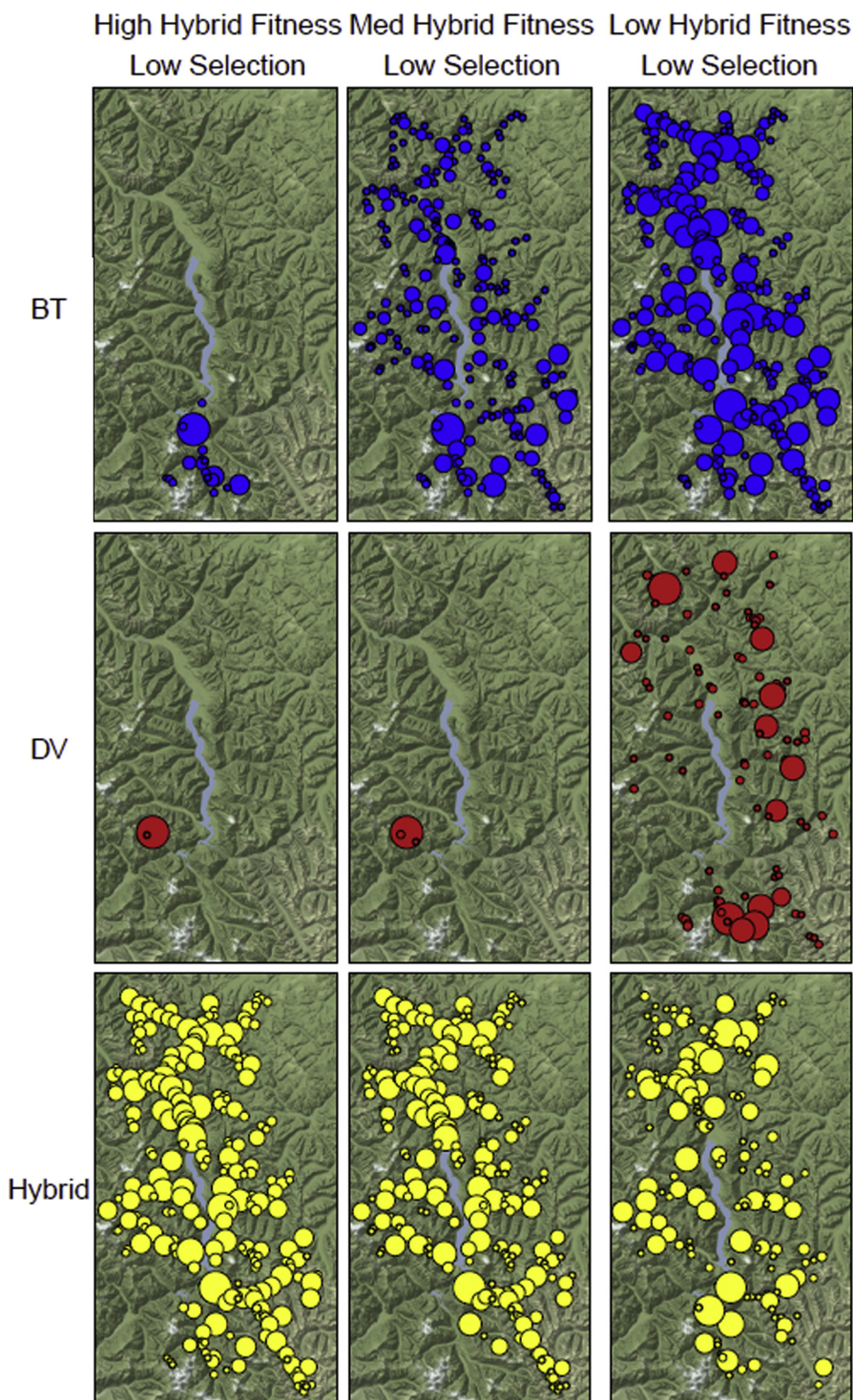


Fig. 6. Spatial distributions of bull trout (blue, top panel), Dolly Varden (red, middle panel), and hybrids (yellow, bottom panel) present in study system patches in the final year of simulation. Model parameters vary across columns, with hybrid fitness decreasing from high (left column) to medium (middle column) to low (right column). For all model scenarios represented in this figure, mating between species was random and temperature-based selection was low. Circles represent patch centroids and circle size is proportional to the number of individuals present in that patch (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

issue further complicated by the complex relationship between genotype and phenotype (vonHoldt et al., 2017). In this study, we used admixture thresholds reported in genetic studies focused on distinguishing hybrids in wild populations (Shepard et al., 2005; Vähä and Primmer, 2006; Harbicht et al., 2014); however, from a conservation perspective, deciding the degree of admixture that influences management decisions is complex and context-specific (Allendorf et al., 2001). Future studies that explore the biological significance of admixture thresholds would provide useful insights for investigations of hybridization dynamics using tools such as our modelling framework.

Future simulation work is also necessary to assess the impact of the

CDMetaPOP mate selection algorithm on simulation results. In the demonstration of our simulation framework, we observed high abundances of hybrids regardless of whether mating was random or with strong preference for mates of the same species. For scenarios where self-preference mating is implemented, mate choice is based on female preference for males within the same natal patch, and that have a similar H index. This relationship assumes that mate pairs are more likely to comprise individuals of similar genotype (e.g. H index), and that genotype is an accurate reflection of phenotype, the primary informant of mate preference in nature. In our simulations, we restricted mate selection to within-patch mating, and instances where only less suitable

males are present (i.e. H indices between female and male are very different) still resulted in the formation of a mate pair. In reality, individuals are likely to make movements to find preferred mates, but how individuals select mates along a spectrum of H indices and phenotypes is unknown. Future applications of our hybridization framework could permit the movement of individuals to neighboring natal patches in instances where mates with preferable H indices are not present in the current patch, and could also explore the relative spawning success of such straying individuals.

#### 4.5. Conclusions

The primary goal of this study was to develop a simulation framework useful for evaluating hybridization dynamics between two species in a heterogeneous system. We accomplished this goal by modifying a previously existing IBM (CDMetaPOP; Landguth et al., 2017b), and by demonstrating a system-specific application of this framework. Such applications of spatially explicit IBMs are increasingly important for forecasting the effects of large-scale processes such as a changing global climate on species distributions and interactions. Additionally, spatially explicit IBMs are useful for predicting the effects of a broad range of potential management and conservation actions. The adaptability of our framework to species- and system-specific characteristics makes it a valuable tool for simulation-based explorations of hybridization dynamics and resulting eco-evolutionary impacts in a variety of contexts.

#### Data accessibility

Simulation input files, summary output data, and R code to replicate all analyses are available online at [https://github.com/lrnathan/EcoMod\\_2019](https://github.com/lrnathan/EcoMod_2019). CDMetaPOP software and user manual are available at <https://github.com/ComputationalEcologyLab/CDMetaPOP>.

#### Author contributions

L. N., H. T., S. G., N. M., K. K., A. M., C. E., E. L. performed all analyses relevant to this study with input from all other authors. L. W., P. S., E. L., E. C., A. B., M.-J. F., and E. L. contributed ideas and feedback central to the development of this study. L. N. and N. M. wrote the manuscript with input from all other authors.

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ecolmodel.2019.03.002>.

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