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Quantifying the Capacity for Assisted Migration to Achieve Conservation and Forestry Goals Under Climate Change

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 **Quantifying the capacity for assisted migration to achieve conservation and forestry goals under climate change Modeling goals of tree assisted migration** 6 Yibiao Zou<sup>1,2</sup>, Gregory A. Backus<sup>1,3</sup>, Hugh D. Safford<sup>1,4</sup>, Sarah Sawyer<sup>5</sup>, Marissa L. **Baskett1** <sup>1</sup> <sup>1</sup>Department of Environmental Science and Policy, University of California, Davis, Davis, CA 95616, USA. <sup>2</sup> Department of Environmental Systems Science, ETH Zürich, Zürich, ZH 8006, Switzerland. <sup>3</sup>Department of Evolution, Ecology and Organismal Biology, University of California, Riverside, Riverside, CA 92521, USA. Vibrant Planet, Incline Village, NV 89451, USA. USDA Forest Service, Washington Office, 1323 Club Dr, Vallejo, CA 94592, USA. Correspondence: Yibiao Zou, phone: +41 762187417, e-mail: [yibzou@student.ethz.ch,](mailto:yibzou@student.ethz.ch) ORCID: 0000-0002-4741- 0934. **Acknowledgement** We thank Dr. Alvaro G. Gutiérrez for sharing the physiological parameters of 20 tree species among the 23 studies species with us. This project was funded by the National Science Foundation grant #DEB-1655475 to MLB. All authors have no conflicts of interest to disclose. We appreciated the feedback from two anonymous reviewers in helping to improve this manuscript. No permits were required for fieldwork. **Abstract** Aim Many tree species may be threatened with declines in range and biomass, or even extinction, if they cannot disperse or adapt quickly enough to keep pace with climate change. One potential, and potentially risky, strategy to mitigate this threat is assisted migration, the intentional movement of species to facilitate population range shifts to more climatically suitable locations under climate change. The ability for assisted migration to minimize risk and maximize conservation and forestry outcomes depends on a multi-faceted decision process for determining, what, where, and how much to move. We provide an assessment on how the benefits and risks of assisted migration could affect the decision-making process. Location

- Mountainous coastal western United States.
- 
- Taxon
- Trees
- 

Methods

### We used a dynamic vegetation model parameterized with 23 tree species.

- Results
- We found that most of the modeled species are likely to experience a substantial decline in biomass,
- with many potentially facing regional extinction by 2100 under the high-emission SSP5-85 climate-change scenario. Though simulations show assisted migration had little effect on the
- forestry goal of total biomass across all species, its effects on the conservation goal of promoting
- individual species' persistence were far more substantial. Among eight assisted migration
- strategies (differing in the life cycle stage of movement and target destination selection criteria),
- the approach that conserved the highest biomass for individual species involved relocating target
- seedlings to areas that recently experienced fire. Although this strategy significantly reduced
- extinction risk for six at-risk species compared to no action, it also slightly reduced biomass of
- four species, due to increasing competition. Species with relatively weak tolerance to drought, fire,
- or high temperature were the most likely candidate groups for assisted migration.
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- Main Conclusions
- Our simulations indicate that assisted migration (AM) can aid conservation by reducing extinction
- risks for species vulnerable to climate change, but it has limited impact on forestry-specific goals,
- affecting overall biomass minimally. This model framework could be applied to other forest
- ecosystems to evaluate the efficacy of assisted migration globally.
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**Keywords:** Assisted migration, dynamic vegetation model, forestry, climate change, range shift,

- biomass loss, management
- 

### **Introduction**

 Climate change poses a significant threat to species unable to adapt, acclimatize, or disperse effectively (Davis Margaret & Shaw Ruth, 2001; Holt, 1990), particularly affecting foundation species like forest trees (Coops & Waring, 2011; Kreyling et al., 2011; Stanke et al., 2021; Tejedor Garavito et al., 2015). This inability can lead to major ecosystem disruptions, as already observed in forests facing severe droughts, altered fire patterns, and increased climate variability (M. I. Williams & Dumroese, 2013). Predictions suggest many tree species' habitats will shift or diminish due to climate change, especially impacting species with poor dispersal abilities, low  acclimatization capacity, or limited genetic diversity, potentially leading to range reduction, biomass loss, or extinction (Nathan et al., 2011; M. I. Williams & Dumroese, 2013; Zhu et al., 2012).

 Assisted migration (AM), or managed relocation, is a proposed strategy to preserve at-risk tree species and ecosystem services by intentionally moving species to more suitable locations (McLachlan et al., 2007; M. I. Williams & Dumroese, 2013). While AM could enhance survival chances of vulnerable species, it is not without risks and has sparked debate over the potential for relocation failures and negative impacts on recipient ecosystems (Champagne et al., 2021; Chen et al., 2021; Hewitt et al., 2011; Kreyling et al., 2011; Minteer & Collins, 2010; Ricciardi & Simberloff, 2009; Richardson et al., 2009; Simler et al., 2019).

 Assisted migration in forest systems can serve either forestry or conservation goals, or potentially both (Pedlar et al., 2012). Among many other objectives, forestry goals often focus on forest productivity, and conservation goals typically focus on species persistence including targets for range and biomass, with diversity potentially connecting to both goals (M. I. Williams & Dumroese, 2013). Though at some level forestry might prioritize the conservation of particular species and conservation may aim to preserve biomass, in this paper we consider "forestry goals" as synonymous with total biomass conservation and "conservation goals" as synonymous with individual species biomass conservation. AM's effectiveness at species or community levels depends on how relocated populations compete with non-target species and contribute to overall system productivity (M. I. Williams & Dumroese, 2013). Achieving conservation and forestry goals through AM, while reducing associated risks, involves decisions about which species to move, when, where, and how. Suitable candidates for AM include species with poor dispersal ability and low tolerance to heat, drought, or fire, given current and expected climate trends (Clark et al., 2016; M. I. Williams & Dumroese, 2013). Current practices often involve moving seedlings grown in greenhouses or direct seed relocation, which might be more cost-effective in some cases but is also prone to higher early-stage mortality (Castro et al., 2023; Clark et al., 2016; Haase et al., 2019; Mohan et al., 2021; M. I. Williams & Dumroese, 2013).

 Selecting target (i.e., destination) locations for AM requires considering proximity to historical ranges, canopy cover, recent disturbances like fire, and balancing AM efforts to enhance success while minimizing competition with local species (Pedlar et al., 2012; Welch et al., 2016). Targeting the closest climatically suitable locations (hereafter, the "minimum-distance" strategy) to the introduced species' historical range could reduce the risk of introducing novel competition to species already extant in the recipient community (Pedlar et al., 2012). Another strategy could be to select locations with low canopy coverto reduce light and water competition ("least- competition") and increase establishment success for AM individuals. Considering disturbance, moving target species to sites which recently experienced fire ("post-fire") could take advantage of fire's reduction of canopy and understory cover, as well as the postfire abundance of bare mineral soil (Welch et al., 2016). Finally, moving species to sites with the least expected fire  frequency ("least-fire") could reduce the potential for fire disturbance to affect establishment success. A dynamic modeling framework that incorporates dispersal and competition dynamics can quantify these aspects to inform AM implementation (Iverson & McKenzie, 2013).

 This study used a dynamic vegetation model modified from ForClim v.3.0 to evaluate forestry and conservation outcomes of AM, focusing on decision-making regarding species selection, timing, location, and intensity of relocation. We parameterized the model with 23 major tree species from the western montane regions of the US (Safford et al., 2021), identifying target species for relocation based on projected population declines under future climate change. We chose our focal species because these species represent an array of life history types with enough data to parametrize our model. Note that we make this choice based on current forest composition rather than current conservation status (i.e. we don't only focus on species with low population sizes), for two reasons. First, we wanted to understand the potential effects of AM of at-risk species on the remainder of the community, so we aimed to include a representative community composition of both at-risk and not-at-risk species. Second, theory indicates that life history susceptibility can serve as a better indicator than current abundance for vulnerability to changing future conditions, and data indicate that even abundant foundation species can experience rapid, unexpected declines under extreme climatic events linked to climate change (Hartmann et al., 2022; Hughes et al., 2017; McPherson et al., 2021; Tilman et al., 1994). We considered four types of AM destination site-selection: minimum-distance (MD), least-competition (LC), post-fire (PF), and least-fire (LF) destinations; and two AM types by relocated life stage: seed AM (DA) and seedling AM (GA). We also explored AM intensity regarding frequency, duration, target locations, and individuals moved. Simulating various climate change and AM management strategies, we measured forestry goals in terms of total biomass and conservation goals in terms of individual species biomass, persistence, and both with biomass-weighted gamma diversity. Our core questions are then (1) for each of (a) forestry and (b) conservation goals, and under a range of climate scenarios, how does the effect of engaging in AM, compared to no action, depend on AM strategy for timing and location, (2) for conservation goals, which types of species most benefit 140 from AM, and (3) how does increasing different aspects of AM intensity affect the outcomes for both target and non-target species?

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Acronym	<b>Full name</b>
AM	Assisted migration
<b>LCDA</b>	Least competition seed assisted migration
<b>LCGA</b>	Least competition seedling assisted migration
<b>LFDA</b>	Least fire seed assisted migration
<b>LFGA</b>	Least fire seedling assisted migration
<b>MDDA</b>	Minimum distance seed assisted migration

**Table 1: acronym summary for management strategies.**



### **Materials and methods**

### **I. Model overview**

 Our model simulates forest dynamics of individual trees, climate change, and management actions in R version 3.6.2. The model has four sub-models that change over each one-year time step: (A) the demographic vegetation sub-model in which we simulate plant growth, mortality, dispersal, and recruitment based on the PLANT sub-model from ForClim v.3.0 (Gutierrez et al., 2016), (2) the assisted migration sub-model in which we simulate several approaches to assisted migration, (3) the climate sub-model in which we simulate changing climatic conditions across the spatial and temporal scale of the model based on estimates from the WorldClim dataset (Fick & Hijmans, 2017), and (D) the fire sub-model in which we simulate fire occurrence and fire-induced tree mortality based on the fire sub-model of ForClim (Figure 2). After introducing our study system and spatial structure, the subsequent sections explain these sub-models.

### **ⅠI. Study system and spatial structure**

 We simulated forest dynamics in a large, mostly forested and mountainous region of the Pacific western United States, ranging from Mediterranean scrub to temperate forests. Trees in this region face increasing risks from climate change, including more frequent and intense droughts and wildfires (Mann & Gleick, 2015; Miller et al., 2009), further exacerbated by human activities (Chen et al 2021). The elevational range of this region is 4 - 4421 m, with a mean of 1313 m. This region is home to several tree species vulnerable to range contraction or extinction due to these environmental changes (Loarie et al., 2008; Rogers et al., 2011). Among these AM candidate species are economically important species such as ponderosa pine (*Pinus ponderosa*) and currently rare species like foxtail pine (*Pinus balfouriana*) (Richardson et al., 2009). Because many of these species take decades to reach maturity (Bonner et al., 2008), urgent conservation may be necessary to prevent extinction and loss of ecosystem services (Stephens et al., 2020).

 We focused on a region made up of two connected line segments (Figure 1, Appendix S1: Figure S1.A), 1 degree longitude in width, following the Sierra Nevada (36°11' N, 119°3' W to 41°23' N, 122°47' W) and the Cascade Range (41°23' N, 122°47' W to 48°36' N, 121°39' W). We 174 divided this area into 1-km<sup>2</sup> grid cells (120 wide and 1311 long), each consisting of 200 175 patches (833 m<sup>2</sup> each) in which we simulated forest dynamics representing the mean dynamics of the entire cell (Gutiérrez et al., 2016). While the spatial location of grid cells is explicit, the spatial 177 structure of patches is implicit. In other words, the 200 patches within each grid cell have no precise

- coordinates, and each of these internal patches share the same climatic conditions based on the
- coordinates of the grid cell. Though there is no direct interaction between patches, seeds can
- disperse between grid cells. In the model simulation, we simplified the spatial structure of the study
- 181 region into a  $1311\times120$  matrix, where the distance between the center of any two neighbor grid
- 182 cells is 30-arcseconds (i.e.,  $\sim$ 1 km).
- At this 1km resolution scale, we used the LEMMA spatial dataset from the year 2017
- (generated from FIA dataset and Landsat imagery) for initial species occurrence and basal area
- estimation (Ohmann & Gregory, 2002), and the WorldClim version-2.1 dataset for elevation data

and climate data (Fick & Hijmans, 2017). We modeled 23 typical tree species from the Sierra

- Nevada and Cascades with accessible physiological parameters (**Table 2**).
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 [double column] Figure 1: Map of our study region. We focused on a region made up of two connected line segments, 1 degree longitude in width, following the Sierra Nevada (in red color, 36°11' N, 119°3' W to 41°23'

- N, 122°47' W) and the Cascade Range (in dark green color, 41°23' N, 122°47' W to 48°36' N, 121°39' W).
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- **Table 2: Species-specific parameter set of 23 tree species used in this study.** Acronyms of columns of traits: minimum growing degree-day requirement (*kDDMins*, °C), drought tolerance (*kDrtols*), fire tolerance class (*kFis*; as class number increases, fire tolerance decreases), minimum and maximum winter temperature tolerances (*kWiTNs* and *kWiTXs,* °C). See Appendix S1: Section S2 Parameterization for parameter value sources, 199 iustification, and calculations.



#### **MODELING GOALS OF TREE ASSISTED MIGRATION**





[double column] Figure 2: Model diagram. The model comprises four interconnected components:

- demographic vegetation, assisted migration, climate, and fire. The demographic vegetation sub-model (A)
- 205 includes four processes:  $(A.a-b)$  reproduction & dispersal,  $(A.c)$  growth, and  $(A.d)$  mortality, with each process
- influenced by local conditions like climate and competition. Reproduction involves a local seed bank and
- stochastic species addition, while dispersal is wind-driven. Growth depends on limiting factors of temperature
- (gDDGF), light (gALGF), and soil moisture (gSMGF), affecting tree size. Mortality arises from baseline rates,
- stress, and fire, with fire tolerance varying by species. Assisted migration (B) is triggered when target species
- biomass falls below a threshold, considering factors like fire risk and competition for destination selection.
- This sub-model, along with climate data, affects fire probability and mortality in the fire sub-model (D).
- Overall, these components are connected by blue arrows, indicating their interdependencies and influence on each other.
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#### **III. Demographic vegetation sub-model**

 In the demographic sub-model (Figure 2.A), we adapted the PLANT sub-model from ForClim v.3.0 , altering only the recruitment function to include a dynamic seed bank influenced by wind- driven seed dispersal (Gutierrez et al., 2016; Rasche et al., 2012). Therefore, seeds can disperse between different grid cells. Growth and mortality functions remained as in the original ForClim model. We focused on long-distance, wind-driven seed dispersal, excluding animal-based dispersal due to limited data. ForClim's effectiveness in predicting forest species composition and productivity under various climates is well-established, as evidenced in previous studies, including those in the western United States (Harald K. M. Bugmann & Solomon, 2000; Gutiérrez et al., 2016).

 The ForClim PLANT sub-model simulates forest demographics in independent patches, accounting for tree recruitment, growth, and mortality. Recruitment depends on local and dispersed seeds, with seedling establishment influenced by species-specific environmental responses (see S1.1.1 Tree reproduction). The model simulates diameter at breast height (*DBH*), tree height, and age for each tree. With this information, we can then compute basal area, woody biomass and foliage biomass based on *DBH* and height, using species-specific allometric equations. We 232 assumed species with basal area higher than a threshold  $T_p$  in a patch have an effective seed bank in that patch to support their presence, where we use the threshold value that provided the highest 234 accuracy of presence-absence predictions under the ForClim framework  $(1 \text{ m}^2/\text{ha})$ ; Gutiérrez et al. 2016). Here we use basal area as a surrogate for biomass (linear approximation, see Appendix S1: 236 Equation S29 & S30) as well as for tree age to reach reproductive maturity, which is a common forestry practice. In addition, we assume that the seed bank persists for the duration of the simulation, for computational simplicity and in line with existing forest dynamic models (Botkin, Janak, & Wallis, 1972; Harald K. M. Bugmann & Solomon, 2000; Rasche et al., 2012); we test the effect of limited seed bank duration in sample model runs (see Discussion). In the growth function, each individual living tree in the model has a chance to increase in diameter and biomass (see

 S1.1.2 Tree growth). The optimum tree growth rate mainly depends on net carbon assimilation, following the carbon budget approach by Moore (1989), while light availability across the crown, growing degree-days (GDD) and drought stress limit the realized growth rate. In the mortality function, each individual living tree can experience mortality based on three mechanisms: baseline mortality, stress-induced mortality, and fire-induced mortality (see S1.1.3 Tree mortality). Individuals experience mortality as a binomial draw weighted by the mortality probability. 248 249 **IV. Assisted migration sub-model**  In the Assisted Migration sub-model of the ForClim framework (Figure 2.B), we focus on the strategic relocation of tree species to new areas in response to declining biomass levels. Following the model developed by (Backus & Baskett, 2021), AM interventions occur when a species' biomass falls below a predefined threshold (see Table 3). The model operates on a cycle of action

255 and rest: relocation actions are taken for a specified number of years  $(I_a)$ , followed by a cooldown<br>256 period  $(I_c)$  of no relocations. This allows the relocated species time to establish in the new 256 period  $(I_c)$  of no relocations. This allows the relocated species time to establish in the new<br>257 environment. The lengths of the action and cooldown periods are consistent across species and are environment. The lengths of the action and cooldown periods are consistent across species and are detailed in Table 3. While the thresholds for implementing assisted migration are deterministic, when AM then occurs then inevitably varies with the variability inherent to the ecosystem (e.g, with fire occurrences and changes in temperature). This approach is analogous to other threshold- based (i.e., based on "trigger reference points" or "decision triggers") approaches to conservation and natural resource management (e.g., harvest control rules dependent on overfishing limits in fisheries, endangered species delisting criteria in recovery plans, or forestry replanting guidelines associated with minimum acceptable stocking rates [live trees per acre] (Cook et al., 2016; Irwin & Conroy, 2013; Stoel, 1978)).

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#### 267 **Table 3: non-species-specific parameters used in the model, symbols used to represent them, values used,**

- 268 **and units of these parameters.** See Appendix S1: Section S1.1 Demographic vegetation sub-model for more
- 269 detailed description and sources of these parameters.



#### **MODELING GOALS OF TREE ASSISTED MIGRATION**



 To estimate suitable target sites for the target species under future climate conditions, we selected grid cells in which the projected bioclimatic conditions in 2100 were within the species' climatic tolerance range. During each year within the relocation period, we set the number of target grid cells for AM as *Ngc*. We simulated AM of two life stages in this sub-model, namely, seed and seedling. We simulated seed assisted migration (DA) by modifying the seed bank (relative recruitment) of the AM target species in the target grid cell, which gives the target species a relative recruitment advantage, namely a 30 times higher recruitment rate than other present species (even if the target species was not already present in the seed bank). For seedling assisted migration (GA), we based our simulation on the common practice in forestry of cultivating seedlings in a greenhouse for several years (Haase et al., 2019) before moving them to a target location. In our model, we simulated this by directly moving a certain number (*Nsd* x 200) of seedlings of the target species with *DBH* = 1.27 *cm* (average size of cultivated seedlings among different tree species (Sáenz-Romero et al., 2021)) into a target grid cell, omitting the greenhouse cultivation processes. The number of seedlings moved to one patch was *Nsd*, while 200 is the number of patches within one grid cell. During an AM period, this sub-model simulates seed or seedling AM on all *Ngc* target grid cells.

 We model four strategies for choosing relocation destinations. Minimum-distance destinations (MD) focus on proximity, selecting grid cells closest to the species' current range. Least-competition destinations (LC) prioritize areas with the lowest existing tree biomass, reducing competition for resources. Post-fire destinations (PF) are areas recently affected by fire within the species' potential range. Least-fire destinations (LF) are the opposite, selecting grid cells with the least recent fire activity, which also generally had the lowest fire probability among the four destination types (Appendix S1: Figure S7). We evaluate each strategy in combination with the two life stages (DA for seeds, GA for seedlings), resulting in eight distinct AM strategies. Additionally, a ninth control strategy (CT) represents a scenario of no action. Our goal is to determine the most effective AM strategy under varying environmental conditions and species- specific factors. The full methodology and detailed analysis of the results are in Appendix S1: Section S1.2.

#### **V. Climate sub-model**

 We used the Environment sub-model of ForClim V3.0 for our Climate sub-model (Rasche et al., 2012). This sub-model calculates basic bioclimatic data needed by the Demographic Vegetation sub-model, namely minimum winter temperature, growing degree days, and drought index, which affect species recruitment, growth, and mortality, as well as fire probability. We calculated the local climate conditions in each cell using raw bioclimatic data from WorldClim. For each cell in our

### model, we calculated the long-term minimum winter temperature as the minimum among the mean

- monthly temperatures of December, January and February over the years 1970-2000. We used the
- mean monthly temperature to calculate the growing degree days, and we used the mean monthly
- temperature and precipitation to calculate the drought index following the methods of Bugmann
- and Cramer (1998) (H. Bugmann & Cramer, 1998). For detailed description of this sub-model, see
- previous research using ForClim (H. K. M. Bugmann, 1996; Harald K. M. Bugmann & Solomon,
- 2000) and Appendix S1: Section S1.3 Climate sub-model.
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### **VI. Fire sub-model**

 In the fire sub-model (Figure 2.D), we simulate tree mortality due to fires in each time step, influenced by the Climate sub-model's environmental inputs. This sub-model consists of two parts: fire regime dynamics and fire-induced mortality. We base fire regime dynamics on the PC2FM model, which calculates annual fire probability within each grid cell using temperature, precipitation, and elevation data (Guyette et al., 2017). When a fire occurs, tree mortality probability depends on the species' fire tolerance class, fire severity, and tree diameter at breast height (*DBH*). There are two types of fire severities: light (ground fires) and severe (stand- replacing crown fires), with an assumed occurrence ratio of 2:1, based on regional empirical data (Safford et al., 2021). Fires affect every tree in a grid cell. We validated the fire sub-model by comparing modelled fire area with the actual fire area from 2001 to 2020 (Appendix S1: Figure S8). Individual trees living in each grid cell then had an additional probability of mortality within the mortality function of the Demographic sub-model (Busing & Solomon, 2006). To determine each tree's chance of mortality, we divided 23 tree species into four fire tolerance classes, based on the categories given by Busing & Solomon (2006) and fire tolerance data from both Busing & Solomon (2006) and the USDA Fire Effects Information System (Cooke et al., 2015). *kFis* is the fire tolerance class of species *s*, with class 1 being the least tolerant and most likely to be killed by fire. All fire tolerance classes except class 1 exhibit a decrease in mortality probability with increasing tree size (i.e. *DBH*). For details see Busing & Solomon (2006) and Appendix S1: Section S1.4.

#### **VII. Model analysis**

 For our model validation, we simulated forest dynamics over a century under the current climate (1970-2000 average) as detailed in Appendix S1: Section S3. In short, we validated the model by testing its performance on reproducing current species distribution ranges and basal area distributions. The model provided relatively accurate predictions on both metrics: the Cohen's kappa values (used to measure the agreement between observed and modelled species occurrence, with values > 0.4 indicating a fair degree of agreement; values < 0.2 indicate performance no better than random) for species-range analysis were greater than 0.2 for 17 out of 23 species, which significantly outperform a locally parameterized dynamic vegetation model (kappa > 0.2 for 9 out

 of 18 species), and are fairly comparable with a regionally parameterized dynamic vegetation 345 model (kappa > 0.2 for 15 out of 18 species) (Cohen, 1960; Gutiérrez et al., 2016). In addition,  $R^2$ for comparison between , predicted basal area vs. observation were higher than 0.3 for 20 out of

23 species and higher than 0.5 for 15 species.

 We then initialized future projections incorporating initial seed banks and fire dynamics, and ran simulations under the eight Assisted Migration strategies plus the no-action control scenario, beginning from the year 2000 across 100 years of climate change. We used 1km resolution climate data from WorldClim data (Fick & Hijmans, 2017) of CanESM5-SSP245 (optimistic, with moderate greenhouse gas mitigation) and CanESM5-SSP585 (business-as-usual emissions) scenarios. We chose CanESM because it provides the projection closest to the average outcomes among ten different climate projection models selected for their historical performance in the region (Pierce et al., 2018; Swart et al., 2019), as we sought to use a more typical than extreme expectation for future climate outcomes. To create an annual time series of climate data across 100 years, we performed a linear interpolation based on climate data of five key years (2000, 2040, 2060, 2080, 2100) for each emissions scenario.

 In our simulation, we begin by establishing an initial seed bank and seeds, utilizing distributions from the LEMMA database. Each simulation time step involves the growth and mortality of stems, as dictated by the demographic vegetation model. Concurrently, we simulate fire events to account for additional mortality due to fire. Following this, new seeds disperse, which leads to updates in the seed bank compositions. If any species' biomass falls below a critical threshold, we relocate it according to the assisted migration strategy being modeled. Finally, the climate changes according to linear interpolations of WorldClim data, and we start the next time step.

 To answer our first question regarding the effect of AM on each of forestry and conservation goals for different AM strategies for location and timing, we conducted 100 replicates for each of the nine management scenarios under each emissions scenario. Outputs measured included total biomass (forestry-focused), species-specific biomass (conservation-focused), and gamma diversity weighted by biomass (relevant to both forestry and conservation). AM's effects on total biomass and gamma diversity were similar, differing from its impact on species-specific biomass. Therefore, we used total biomass and gamma diversity for forestry outcomes and focused on species-specific biomass for conservation outcomes.

 We then analyzed the best-performing strategy, PFGA, under the CanESM5-SSP585 scenario, to explore the traits that influenced which species most benefited from AM and the effect of AM intensity. We chose this scenario for its sufficient climate change impacts on species-level biomass, allowing for a meaningful analysis of AM strategies. To answer our second question regarding which types of species most benefit from AM, we performed a principle components analysis of the average number of relocations per species as it depended on climatic-tolerance parameters (minimum growing degree-day requirement, drought tolerance, fire tolerance, and

- minimum/maximum winter temperature tolerances). To answer our third question regarding the
- effects of different aspects of AM intensity, we varied AM intensity in terms of the frequency and
- 384 duration of AM actions (values of  $I_c$  and  $I_d$ ) and the number of seedlings ( $N_{sd}$ ) and target sites ( $N_{sd}$ )
- implemented.
- **Results**

#### **Forestry-oriented outcomes**

 On average, the total biomass decreased by ~70% over the 100 years of simulated climate change in the higher emission SSP585 scenario, regardless of management approach (Figure 3). By contrast, gamma diversity remained almost the same as the initial state in the SSP585 scenario. Under the SSP245 scenario, both total biomass and gamma diversity in 2100 remained almost the same as the conditions in 2000. Different AM strategies had a negligible effect on total biomass and gamma diversity. This lack of difference occurs because, while AM can affect individual species' outcomes for a few particularly vulnerable species as detailed below, without AM affecting those species, growth in other species with less vulnerability to climate change counterbalances the loss of vulnerable species to lead to little change in community-level biomass- based metrics. Therefore, for our forestry-oriented metrics (question 1(a)), AM had little effect on the outcome compared to no action, regardless of AM strategy (Figure 3).





 **[double column] Figure 3: Forestry-oriented outcomes using different AM strategies under two climate change scenarios**: **SSP245 (moderate climate change; circles) and SSP585 (business-as-usual climate change; triangles)**. (A) Relative change in biomass from initial biomass (the biomass of all trees after 100 years relative to the initial biomass), and (B) gamma diversity by biomass ratio over the same period. Results show

 average values with standard deviation. AM strategies are grouped by destination criteria (LC: least-competition; LF: least-fire; MD: minimum-distance; PF: post-fire) and method (seeds: DA, seedlings: GA), including a control group (no intervention: CT).. **Conservation-oriented outcomes** Under the SSP245 climate scenario, about half of the simulated species decreased in biomass, while the other half increased (Figure 4). Species like *Quercus kelloggii* (species 22), *Acer macrophyllum* (5), *Arbutus menziesii* (6), and *Calocedrus decurrens* (18), with their relatively high tolerance to drought, heat, and fire (Figure 4), showed biomass gains. A few species, such as *Chamaecyparis nootkatensis* (7), experienced declines below the level that triggered AM actions (Figure 4). In contrast, in the SSP585 scenario, 14 species experienced significant (>70%) biomass reductions (Figure 4). Seven of these, including various *Abies* and *Picea* species, faced a high risk of local extinction, with over 90% biomass decrease. They frequently fell below the AM action threshold. 



 **[double column] Figure 4: Conservation-oriented outcomes of biomass for the control group (no AM) in simulations under SSP245 and SSP585 climate change scenarios**. The y-axis indicates relative change in species-specific biomass from initial biomass (the biomass of all trees after 100 years relative to the initial 429 biomass). Blue bars indicate simulations with dispersal (mean  $\pm$  sd), red bars without. Red dashed lines mark the AM threshold. Species IDs on the x-axis are ordered by mean biomass ratio under SSP585 emission scenario. 

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 **[double column] Figure 5: Conservation-oriented outcomes using different AM strategies under two climate change scenarios: SSP245 (left column) and SSP585 (right column)**. Relative effect of AM on biomass (species-specific biomass in 2100 under each AM strategy divided by species-specific biomass without AM) are shown on a log10 scale; horizontal dashed lines indicate equal biomass with and without AM. If the biomass ratio > 1 for an AM strategy, it means it performs better than no AM actions. Dot/bar colors represent the frequency of AM for each species, and shapes in panels A-D indicate AM strategies. Panels A-B and C-D display relative effects for AM at seed and seedling stages, respectively, averaged over 100 repetitions. Panels E-F feature boxplots of relative effects under the optimal post-fire seedling AM strategy (PFGA). Species identities for x-axis numbers are in Table 2. Effects of AM are small except for species 7, 3 and 4 under SSP585 scenario.

 Throughout the simulations, 15 out of 23 species underwent relocation at least once (Figure 5). However, only a few, such as *C. nootkatensis* (7), *Abies lasiocarpa* (3), and *A. procera* (4), consistently benefited from AM, with *C. nootkatensis* (7) showing the most significant improvement, especially for SSP585 (Figure 5.B,D,F). On the other hand, *Abies concolor* (16) displayed lower biomass under some AM strategies compared to no action.

 For SSP585, post-fire seedling AM and post-fire seed AM were generally the most effective strategies in increasing species-specific biomass (Figure 5.B&D).. For SSP245, the least- competition seed or seedling strategies were the most effective strategies (Figure 5A&C), but their effect on target species' biomass was much smaller than the effect of AM on biomass for SSP585. Overall, for our conservation-oriented metrics (Question 1(b)), the effectiveness of AM varied by climate scenario, AM strategy, and species, with only a subset of species showing substantial benefits under more extreme climate change (Figure 5), highlighting the role of targeted and species-specific AM strategies under different climate change scenarios.

#### **Types of species that benefit from AM**

 For the most effective AM strategy (post-fire seedling AM), our principal component analysis showed that species that were often relocated in our model had similarly low values on dimension 1, which accounted for 79.7% of variance (Figure 5). Low values in dimension 1 implied species were drought-intolerant, fire-intolerant, and cold-adapted. Accordingly, *C. nootkatensis* (7), one of the least drought/fire-tolerant species, benefited the most from AM as noted above (Figure 5). Conversely, species like *A. macrophyllum* (5), with high drought and heat tolerance, thrived under future climate conditions (Figure 4). In sum, our analysis found that species which are poorly adapted to drought, fire, and warmer conditions were more likely to face local extinction without AM intervention and to benefit from AM intervention compared to other species we modeled (Question 2; Figure 6).



 **[single column] Figure 6: Principal component analysis of species-specific climatic-tolerance parameters.** Dot colors represent the average number of relocations per species under the post-fire seedling AM strategy (PFGA) over 100 repetitions, with numbers indicating tree species. More relocations suggest higher local extinction risk. Parameters include minimum growing degree-day requirement (kDDMin), drought tolerance (kDrTol), fire tolerance (kFi), and minimum/maximum winter temperature tolerances (kWiTN, kWiTX). Tree species identities for each number are detailed in Table 2.

### **AM intensity**

 In the analysis of different AM durations, neither years per relocation nor minimum years between relocation had a prominent effect on the total biomass ratio and gamma diversity by biomass (see Appendix S1: Figure S8). More consecutive years per relocation and fewer years between relocations increased the biomass ratio of *C. nootkatensis* (7, Figure 7.A), and *A. procera* (4, Appendix S1: Figure S5). AM strategies with more seedlings and more destinations increased the biomass ratio of *C. nootkatensis* (7, Figure 7.D), *A. amabilis* (1), *A. lasiocarpa* (3) *and A. procera* (4) (Appendix S1: Figure S6). These species are all AM target species with weak heat, fire, and/or drought tolerance. In comparison, species with more moderate-to-high tolerances (e.g., *A. concolor,* Figure 7.B&E and *P. balfouriana*, Figure 7.C&F) displayed no consistent trends in response to increased AM intensity, neither benefitting significantly nor experiencing adverse effects. Therefore, multiple approaches to increasing AM intensity benefited at-risk species, with minimal effects on non-target species (Question 3; Figure 7).

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 **[double column] Figure 7: The effect of AM intensity on conservation-oriented outcomes of PFGA under the CanESM5-SSP585 scenario.** Panels A-C depict color maps illustrating species-specific biomass ratios (biomass in 2100 using post-fire seeding (PFGA) divided by biomass with no AM). These maps focus on the effects of years per relocation and minimum years between relocations on three species with varying tolerances: *Chamaecyparis nootkatensis* (low tolerance to heat, fire, drought), *Abies concolor* (moderate tolerance), and *Pinus balfouriana* (moderate drought, high fire tolerance). Panels D-F assess how the number of relocated seedlings and target sites influence species-specific biomass ratios for these species..

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#### **Discussion**

 Our simulations indicate that assisted migration can aid conservation by reducing extinction risks for species vulnerable to climate change, but it has limited impact on forestry-specific goals, affecting overall biomass minimally. The effect of AM arises from the significant impacts of climate change on montane forests in the western United States predicted by our simulations. 511 Under the SSP585 scenario, we observed a dramatic ~70% decline in total tree biomass. Conversely, under the SSP245 scenario, biomass and gamma diversity showed little change. Previous studies support these findings. Loarie et al. (2008) predicted major range reductions for numerous endemic plant species in California and southern Oregon due to climate change. Lenihan et al. (2008) and Rogers et al. (2011) forecasted potential net carbon losses in California forests by 516 2100, depending on the climate scenario. In contrast, Zhu et al. (2018) suggested a possible ~40%

increase in forest biomass in Sierra Nevada and Cascades by 2080 under the RCP8.5 scenario, due

- to warming and forest recovery from agricultural land. However, this study did not account for
- disturbances like fires, insect outbreaks, and drought. Recent data shows a 6.7% loss in California
- forest cover from 1985 to 2021, mainly due to wildfires (Wang et al., 2022). Additionally, Steel et
- al. (2022) reported that 30% of conifer forests in the southern Sierra Nevada transitioned to non-
- forest vegetation between 2011-2020, primarily due to drought-related tree mortality and wildfires.
- While future forest biomass trends carry some uncertainty (Lenihan et al., 2008; Zhu et al., 2018),
- the majority of projections and trend analyses suggest a significant decline in biomass (Rogers et al., 2011; Wang et al., 2022; J. N. Williams et al., 2023), underscoring the potential value of management strategies like assisted migration.
- Our simulations showed that under a business-as-usual climate scenario, 15 out of 23 species would face significant biomass reduction. This aligns with previous studies that have documented population declines in similar species due to climate-induced disturbances(Coops & Waring, 2011; Loarie et al., 2008; Stanke et al., 2021). For instance, Stanke et al. (2021) noted declines in *A. lasiocarpa*, *P. engelmannii*, and *P. contorta latifolia*, while Coops & Waring (2011) predicted a 40%-50% range reduction for *P. contorta latifolia* and *P. ponderosa* by 2080 in the Northwestern
- US under similar climate scenarios, assuming no dispersal.
- AM in our simulations effectively reduced extinction risks for certain species by enhancing their biomass. *C. nootkatensis* (7), for example, showed significant biomass increases (60% and 120% higher than no action scenarios under optimistic and business-as-usual climates, respectively). AM also supported biomass retention in *A. lasiocarpa* (3) and *A. procera* (4) under the business-as-usual scenario. However, the overall ecosystem impact of AM was limited, resulting in only slight increases in total biomass and gamma diversity.
- Interestingly, AM led to biomass declines in four species, possibly due to increased competition from other relocated species. The most significant conservation benefits of AM were observed for species intolerant to fire, drought, and heat, particularly when targeting post-fire locations and implementing AM with greater frequency, number of relocated individuals, and number of target locations.
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### *Candidate species for AM*

 Our model identified species with low tolerance to drought, fire, and high temperature as the most vulnerable species to climate change, making them prime candidates for AM to be relocated to more climatically suitable habitat. This aligns with predictions from previous Species Distribution Models (SDMs) that these species may face severe declines in biomass and range under a business-as-usual climate scenario (Coops & Waring, 2011; Stanke et al., 2021). Our dynamic model, accounting for competition and dispersal, suggests that natural dispersal is too slow to keep pace with rapid climate change for these at-risk species (Figure S10), reinforcing findings from earlier studies.

 In our model, these at-risk species with low tolerance to fire, drought, and/or heat then benefited most from AM. To identify potential AM candidates in other ecosystems, one could employ a phylogenetic approach to pinpoint clades sensitive to these stresses (Niinemets & Valladares, 2006). Alternatively, a trait-based analysis could estimate climatic tolerance for each tree species. For instance, thin bark is often a marker of low fire resistance (Kidd & Varner, 2019; Stevens et al., 2020), so species with such traits could be considered for AM in systems with fewer available data. Note that these suggestions are speculative and require further research to validate their effectiveness before implementation in forest management practices.

### *Optimal approaches for AM*

 In our model, the most effective AM strategies were post-fire seedling AM and post-fire seed AM (Figure 5). These methods likely do well due to reduced establishment failure and reduced competition for transplanted trees. In our model, the effectiveness of seed dispersal (e.g., via drones) post-fire was comparable to moving greenhouse-cultivated seedlings, suggesting an alternative to the conventional approach. However, current seed-based propagation has seen limited success in forestry, and drone-based seeding lacks definitive field-based analysis of success (Castro et al., 2023).

 Seedling survival and growth are typically hindered by surrounding vegetation (due to light competition) and are enhanced by canopy openness (Berkowitz et al., 1995; Duclos et al., 2013; Gerhardt, 1996). Our post-fire AM strategies target recently burned areas with lower biomass and higher canopy openness (Figure S7), providing relocated seeds or seedlings with more light and other resources. Although our model does not account for water competition, soil water availability is also often higher in recently burned forests, where water withdrawals by living vegetation have been reduced (e.g., (Cardenas & Kanarek, 2014)). At the same time, water stress in exposed, highly insolated burned sites can be very high in the dry season, negatively impacting seedling survival (Shive et al., 2018); our model does not account for topographically driven soil water availability. Least-competition AM strategies also performed well, targeting areas with minimal biomass and hence reduced competition. However, these strategies often relocate species to higher elevations with less suitable temperatures (Figure S7), slightly diminishing their effectiveness compared to post-fire AM.

#### *Accounting for the risks of AM*

 Our model highlights two risks of assisted migration: establishment failure for target species and increased competition with non-target species. For instance, *A. grandis* (2) showed no biomass change during simulations, suggesting establishment failure. This is likely due to harsh 2100 climates under the SSP585 scenario, with suitable habitats shifting outside our study region, as also projected in other studies (Coops & Waring, 2011). Such conditions may permit survival but hinder seedling establishment. Identifying species unlikely to benefit from AM is as crucial as finding suitable targets, considering AM's costs.

 Additionally, our model indicates increased competition risks to non-target or target species. For example, under all eight AM strategies in the SSP585 scenario, *A. concolor* (16) and *P. jeffreyi* (19), predominantly located in southern California and the Sierra Nevada, showed reduced biomass compared to no action. This decrease might result from establishment failures at AM destinations and increased competition from other AM-targeted species within their current range. 

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### *Potential effects of model assumptions*

 Our model, while comprehensive, is based on several simplifying assumptions, which can inevitably affect our conclusions. First, our climatic data resolution is 1km, which averages over microclimatic variations (i.e., due to elevational or topographic changes) that affect tree demography (De Frenne et al., 2019; Fick & Hijmans, 2017). Cooler, wetter microclimates can buffer macroclimate effects, potentially leading our model to overestimate negative climate change impacts on seedling/sapling survival and, consequently, forest biomass and range loss. On the other hand, assisted migration strategies that are focused on relocation to open-canopy areas, such as the least-competition and post-fire strategies, will likely be riskier in warmer, drier microclimates. Our model ignores microclimatic variation on the landscape, and assumes that dry and moist microclimates balance each other out at the landscape scale.

 Second, due to the lack of data, our model does not include the effects of non-fire disturbances, such as those arising from pests, pathogens, or seed predators, despite their significant role in forest dynamics (Bentz et al., 2010). In particular, we did not model bark beetles and diseases like white pine blister rust and Sudden Oak Death, which are prevalent in the North American Mediterranean Climate Zone (NAMCZ) (Berner et al., 2017; Negrón et al., 2009). This exclusion likely leads to an underestimation of tree mortality and extinction risks, and therefore a potential underestimation in AM frequency. Bark beetle and disease susceptibility could also be considered in choosing AM target locations to minimize infection risks, but this raises the issue of potentially spreading diseases through translocated seedlings. Furthermore, our model's coarse scale does not account for the critical role of soil microsites in seed germination and survival (Castro et al. 2023). Incorporation of these additional drivers of forest dynamics and their connections to climate change could expand the primary factors that influence vulnerability to climate change beyond the three modeled here (drought, fire, and temperature tolerance).

 Third, our study's spatial limits are defined by geographic and political boundaries, not ecological properties. This limitation is especially relevant for species like *A. lasiocarpa* in the western United States, where suitable habitats for northward movement are scarce. Cross-border coordination, such as with Canada, could potentially increase the persistence of northern species, aiding conservation goals (Schwartz et al., 2012; Vitt et al., 2010).

 Fourth, our model presupposes that tree seeds, once deposited, can persist in the seed bank through the entire duration of the 100-year simulation. Forest dynamic models frequently assume indefinite seed longevity for computational ease and due to the absence of detailed seed longevity data for most species (Botkin et al., 1972; Harald K. M. Bugmann & Solomon, 2000; Rasche et al., 2012). However, empirical evidence suggests that most tree seeds do not survive more than a year or two under typical field conditions (Davies et al., 2020; Mame et al., 2019; Nadarajan et al., 2023). Therefore, the persistent seed bank assumed here could lead to an overestimation of recruitment success, thereby potentially inflating the projected biomass for certain species. To evaluate the impact of our assumption regarding long-term seed viability on our conclusions, we conducted a series of simulations with a one-year seed bank duration under the SSP585 emission scenario. The outcomes mirrored the patterns observed in Figures 2 and 4 (Figure S9). We interpret this consistency to stem from the strong filtering effects of climate and light conditions on plant growth and survival, such that these processes are the primary drivers of which species establish and outweigh any effect of seed bank availability.

 Lastly, our model does not account for the potential of phenotypic and genetic adaptations in tree species, which might reduce extinction risk and the need for AM under climate change (Chown et al., 2010; Nicotra et al., 2010). Short-term phenotypic changes, such as increased root-to-shoot ratio for water efficiency (Nicotra et al., 2010), and long-term evolutionary adaptations are crucial considerations (Alberto et al., 2013). The concept of assisted gene flow, moving locally-adapted genes within species ranges, emerges as an additional strategy for dispersal-limited species, warranting further investigation in future studies incorporating evolutionary dynamics (Aitken & Bemmels, 2016; Kelly & Phillips, 2019; Young et al., 2020).

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- *Model applications to other settings*

 Applying our approach in new geographic locations to evaluate conservation performance of AM strategies requires data on species-specific physiological parameters (see Table.S1), which might be available in the literature or the TRY dataset (Kattge et al., 2020), as well as data on species occurrence and climatic tolerance traits. The European Alps are one candidate location for implementing this framework to evaluate AM performance, because these parameters are available for hundreds of European tree species (H. Bugmann, 1994). To inform management of climate- threatened species in more data-poor locations, future research could focus on our broader take- home messages of which species could be candidate functional types for AM (e.g., species intolerant to fire, drought, or heat, depending on which environmental factors climate change is impacting and how in a given location) and the effects of inter-specific competition on AM risks and benefits.

#### **Open Research Statement**

 The major code (novel) and example data to replicate the results in this paper are on the GitHub repository: [https://github.com/Yibiaozou/UCDavis\\_Forest\\_AM,](https://github.com/Yibiaozou/UCDavis_Forest_AM) which is also the intended repository for permanent archive. Observation data and climatic data used in this paper are already published and publicly available, with those items cited in this submission. Tree observation data in year 2017 was downloaded from LEMMA [\(https://lemmadownload.forestry.oregonstate.edu/\)](https://lemmadownload.forestry.oregonstate.edu/) using the following query: [BA\_GE\_3, ABAM\_BA, ABGRC\_BA, ABLA\_BA, ABPRSH\_BA, ACMA3\_BA, ARME\_BA, CHNO\_BA, PIEN\_BA, PICO\_BA, PIMO3\_BA, PIPO\_BA, PSME\_BA, QUGA4\_BA, TSHE\_BA, TSME\_BA, CADE27\_BA, PIJE\_BA, PILA\_BA, PIAL\_BA, QUKE\_BA, PIBA\_BA]. For climatic data, we used WorldClim version-2.1 [https://www.worldclim.org/data/cmip6/cmip6\_clim30s.html]. For burned-area data, we used observation from Williams et al. (2023) on Dryad [https://doi.org/10.25338/B8TP97].

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