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Disturbance and climate microrefugia mediate tree range shifts during climate change

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Abstract

Context Many tree species will shift their distribution as the climate continues to change. To assess species' range changes, modeling efforts often rely on climatic predictors, sometimes incorporating biotic interactions (e.g. competition or facilitation), but without integrating topographic complexity or the dynamics of disturbance and forest succession.

Objectives We investigated the role of 'safe islands' of establishment ("microrefugia") in conjunction with disturbance and succession, on mediating range shifts.

Methods We simulated eight tree species and multiple disturbances across an artificial landscape designed to highlight variation in topographic complexity. Specifically, we simulated spatially explicit successional changes for a 100-year period of climate warming under different scenarios of disturbance and climate microrefugia.

Results Disturbance regimes play a major role in mediating species range changes. The effects of disturbance range from expediting range contractions for some species to facilitating colonization of new ranges for others. Microrefugia generally had a significant but smaller effect on range changes. The existence of microrefugia could enhance range persistence but implies increased environmental heterogeneity, thereby hampering migration under some disturbance regimes and for species with low dispersal capabilities. Species that gained suitable habitat due to climate change largely depended on the interaction between species life history traits, environmental heterogeneity and disturbance regimes to expand their ranges.

Conclusions Disturbance and microrefugia play a key role in determining forest range shifts during climate change. The study highlights the urgent need of including non-deterministic successional pathways into climate change projections of species distributions.

Keywords Climate change · Forest dynamics · LANDIS-II · Range change · Succession

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Introduction

Climate represents a major driver of plant distributions (Woodward 1987), but it is not the only determinant.

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Vegetation distribution is not in equilibrium with climate alone (Svenning and Sandel 2013), i.e., climate does not fully explain variation in species' distributions. Climate has usually been conceptualized as a driver operating over large geographical scales (see Franklin 2010 for different conceptual frameworks); however, recent research demonstrates that even at large scales, geographic distributions of tree species may be constrained by factors other than climatic suitability within species' range (Serra-Diaz et al. 2013). For instance, biotic interactions help explain the distribution of species over large extents (Wisz et al. 2013), and species' traits, such as dispersal, play a significant role in shaping patterns of distribution and abundance (Gilbert et al. 2004; Boulangeat et al. 2012). In fact, modeling experiments suggest species migration is occurring even in the absence of a projected climate change, due to species distributions currently being 'out of equilibrium' with climate (García-Valdés et al. 2013). Therefore, a general understanding of the emergent properties derived from multiple mechanisms involved in species' range dynamics is urgently needed.

One of the main mechanisms driving species distributions are disturbance regimes. Disturbance (or its absence) is a large-scale driver of species composition worldwide (Bond and Keeley 2005) and a crucial driver of vegetation changes in the face of global change (Sykes and Prentice 1996; Opdam and Wascher 2004; Scheiter and Higgins 2009). Disturbance affects species' distributions in many ways. For example, disturbance may promote the removal of vegetation through species' mortality or changes in stand structure (e.g. a reduction in crown cover), thereby opening space and changing light or soil conditions and enabling other species to establish (Galiano et al. 2010). The composition of post-disturbance vegetation will also depend upon how well the disturbed species recover and compete with new arrivals, which is typically a function of their life history traits (Pickett 1985). As a result, forecasts of species' distributions should account for rapid climatic changes (Loarie et al. 2009) together with the inherent disturbance and non-equilibrium dynamics, which are likely to be more prevalent in the forthcoming decades (Sala 2000; Renwick and Rocca 2015). Indeed, many studies highlight large-scale synergistic effects of climate change and human-caused disturbances such as land use change (Syphard et al. 2011; Beltrán et al. 2013) or land management hampering species

recruitment in certain locations (Munier et al. 2010; Boulangeat et al. 2014); these anthropogenic disturbances can interact with existing climatic gradients (McLaughlin and Zavaleta 2013; Cohn et al. 2013) impeding or enhancing species turnover.

In contrast with the dynamic nature of disturbance and climatic change, relatively static landscape features may mediate the potential for species' distributions to shift under climate change. That is, patches with suitable habitat for some species may persist during unfavorable or rapidly changing regional conditions. Many paleoecological studies show that such "*safe islands*" existed in the past (Mosblech et al. 2011; Keppel et al. 2012) and may play an important role in the future (Hannah et al. 2014). These "refugia" are often found in places with relatively greater landscape heterogeneity (Rull 2009), where fluctuations in environmental conditions occur at high spatial frequencies, for example in mountain ranges. In this paper we will refer to relatively small patches of climatically suitable habitat, such as those that would be produced by topographic effects on local climate, as climate microrefugia (distinct from e.g. edaphic refugia or disturbance refugia). Examples include valley bottoms or north-facing slopes where cold air pooling or topographic shading lead to cooler, moister conditions compared to those found in the surrounding landscape matrix (Dobrowski 2011; Dingman et al. 2013; Curtis et al. 2014).

The interaction between disturbance dynamics and persistence due to microrefugia has rarely been examined [but see Vanderwel and Purves (2014)]. Studies suggest that rapid species migrations can be achieved through disturbances (Johnstone and Chapin 2003) combined with locally heterogeneous climate conditions and the presence of climate refugia, areas where conditions are suitable for persistence (Vanderwel and Purves 2014). On the other hand, disturbance could be considered as a range maintaining process for disturbance-adapted species (e.g. disturbance refugia). In addition, the amount of suitable microrefugia depends on the physical conditions of the landscape, which may also co-vary with characteristics of disturbance regimes and other factors (e.g. climate, urbanization; Krawchuk and Moritz 2011). The relative importance of these two mechanisms may then be dependent on how extensive microrefugia and disturbances are in space or time. Therefore, there is a need to assess different scenarios of spatial and

temporal distributions of microrefugia and disturbance regimes to clarify the role of both disturbance and microrefugia in mediating range shifts.

In the case of forests, tree range dynamics present several challenges. Trees are long-lived organisms that tend to be resilient to climate extreme events during their adult stage (Lloret et al. 2012). This creates an extinction debt in which climatic suitability may eroded along the trailing edge of a tree species range but individual trees may persist for decades or centuries (Vellend et al. 2006). The resilience of adult trees contrasts with the sensitivity of trees during their early life stages when survival is low. Hence, the recruitment phase is key to understanding patterns of species co-existence (Grubb 1977; Clark and Clark 1992; Sánchez-Gómez et al. 2006; Galiano et al. 2010), and future distributions will likely depend upon landscape heterogeneity protecting population relicts and disturbance regimes favoring or hampering establishment. Large scale recruitment failures have already been observed leading to species compositional turnover in forests (Carnicer et al. 2014). Integrating demographic and community dynamics operating at different time scales in a successional framework allows us to examine these key processes involved in species' redistributions (Walker and Wardle 2014).

In this study, we examined how different disturbance regimes and patterns of climate microrefugia influence shifting distributions of tree species during climate change. We modeled range change on an elevation gradient for eight interacting tree species with contrasting strategies in terms of environmental adaptation, colonization ability, and dispersal distance. Range changes were simulated under different disturbance regimes and spatial arrangements of microrefugia in order to understand: (1) How does disturbance shape tree species range under a directional shift in climate conditions? (2) How does landscape heterogeneity shape range changes? (3) What are the interactions and trade-offs between disturbance regimes, the availability of climate microrefugia and species traits?

Methods

Simulated species characteristics, initial distribution and geographical setting

We parameterized eight species interacting across a landscape represented by a simple spatial gradient characterizing elevation in mountainous terrain (e.g. Franklin et al. 2001). We represented key traits that determine tree species response to climate and relative competition abilities to other tree species. We parameterized these species (or functional types) with orthogonal combinations of (1) climatic niche: cold or warm adapted, determined by probabilities of establishment in the simulated landscape; (2) shade tolerance: shade tolerant or shade intolerant affecting establishment and survival when other species are present; and (3) dispersal ability: long or short distance. We acknowledge that most traits are correlated and do not represent orthogonal combinations as in our experiment here. However, such combination can help us determine relative trade-offs in the different scenarios simulated. Other species traits (growth rate, longevity) were identical among species to focus our simulations on those traits hypothesized to strongly affect range dynamics in a rapidly changing climate (see full parameters for species characterization in Electronic Supplementary Material 1).

Species were located in a landscape represented by a cellular grid of 100 row by 100 columns (10,000 cells). The experimental landscape represented a simplified mountain hill slope, whereby the y-axis of the gridded landscape depicts the environmental gradient (i.e., increasing elevation with a corresponding temperature gradient from warmer to colder) and no environmental variation along the x-axis (Fig. 1). Species were initially distributed along the y-axis according to their environmental adaptation (cold or warm adapted). Therefore, the probability that each species was initially found in a cell was dependent on the cell's relative location along the y-axis (Fig. 1). Initial location probabilities followed normal distributions that were centered in rows 75 and 25 for cold and warm species, respectively, with standard deviation of 10 cells. This initial configuration was designed to generate a gradient of warm adapted species at low 'elevations' (low values along the y-axis), a transition zone or ecotone (middle elevations), and cold adapted species located at high elevations (cells with high y-axis values). Each species initially occupied 40 % of the total available landscape, a high degree of forest occupancy in the landscape. Consequently, the results of the simulation should be understood in the context of an initial configuration of a mixed dense forest. Initial species' age was randomly assigned (1–100 years) to each species in each cell.
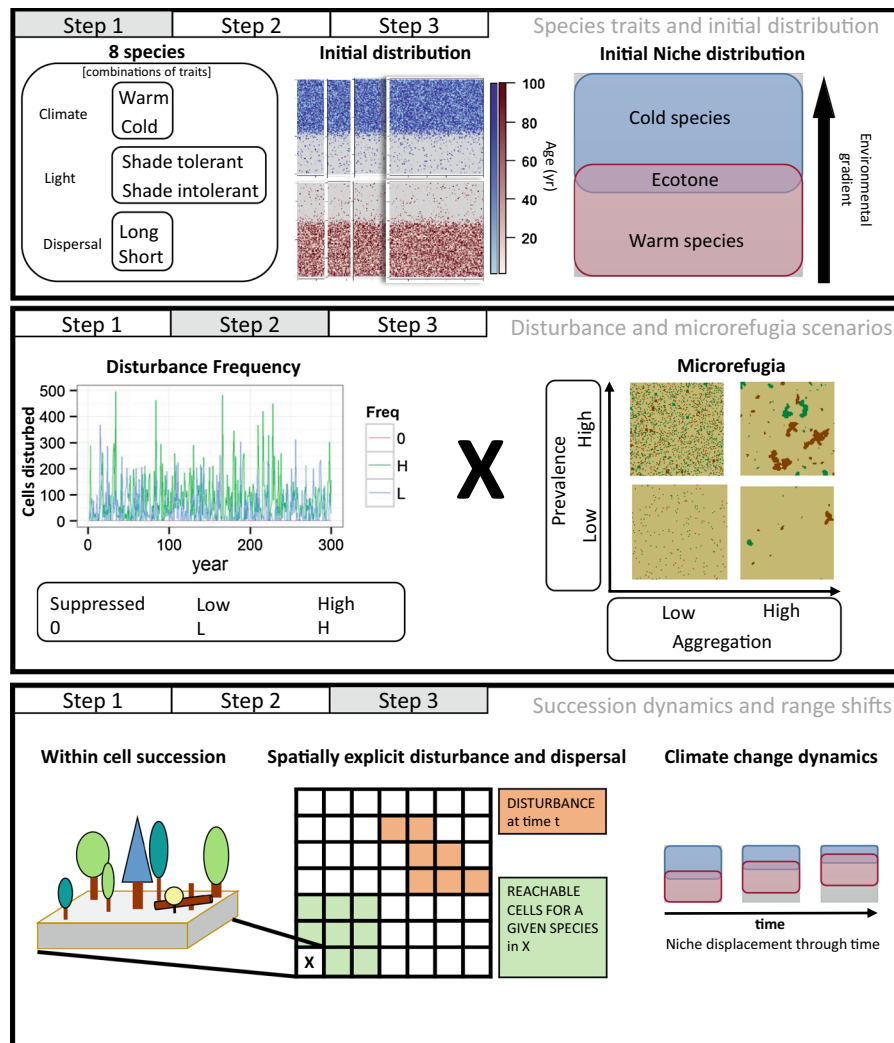
Fig. 1 Sequence of model building in three steps: (step 1) Design of eight species and initial distributions in a square study area of 100×100 cells. Initial distributions according to a normal distribution across a vertical environmental gradient; (step 2) design of several scenarios involving disturbance and climate microrefugia arrangements; (step 3) simulation of succession dynamics over time in a dynamic climate. Succession rules are cell based (see http://www.landis-ii.org/ for further details); while other ecological processes operate spatially across cells. Climate change affects species by displacing niche upwards

Succession and range dynamics

We simulated species range dynamics using LANDIS-II (v. 6.0; http://www.landis-ii.org/; Scheller et al. (2007)), a landscape disturbance and succession model. The model simulates forest dynamics, taking into account tree cohort establishment, growth and mortality within each cell of a gridded landscape. The model does not apply these processes to individuals but rather uses cohorts, an aggregation of individuals of the same age

(or class) in a grid cell. Therefore it is assumed that cohorts possess the same resource demands and disturbance vulnerability. In addition, other spatially explicit processes are simulated, including seed dispersal and disturbances. The latter can be modeled from a wide range of available libraries (see http://www.landis-ii.org/ extensions for further details). In our simulations, we used an annual time step.

We simulated succession using the Biomass Succession extension for LANDIS-II (Scheller and Mladenoff

2004). This extension grows each species-age cohort according to a maximum growth rate and depends upon age and competition with other cohorts in the cell. A cohort gains aboveground biomass (g m^{-2}) over time; density of stems is not tracked. Cohorts compete for 'growing space' with other species and other age cohorts. Cohorts are added to a cell if propagules are available from the surrounding cells (dependent on seed dispersal distances), if understory light is sufficient for the species (dependent on shade tolerance) and if and the probability of establishment (P_est) is greater than a random uniform number (0–1.0). Mortality is governed by self-thinning early in succession and age-dependent mortality later (Scheller and Mladenoff 2004). We assigned all simulated species an identical maximum growth rate of 100 g m^{-2} year^{-1}. P_est was determined by each species' climatic tolerance and location within the landscape (see below).

Simulation scenarios

We simulated a total of 15 scenarios corresponding to a combination of three disturbance frequencies (suppressed, low frequency and high frequency) and five microrefugia levels (no microrefugia plus four combinations of total area of microrefugia and aggregation of microrefugia patches) (step 2 in Fig. 1). Each scenario was run several times using a different initial distribution of species (five replications) and microrefugia distribution (five replications in scenarios with microclimates) to account for the variation in the stochastic nature of initial species' distributions, microrefugia random configuration and stochastic model components. The total number of simulations including replication was 315. We did not include scenarios without climate change as our goals were to investigate the effect of disturbance and microrefugia on vegetation redistribution in a dynamic climate.

Species range change was calculated for each species. We plotted the ratio of area change relative to time 0 along the simulation timeline. This allowed us to examine the effect of disturbance and microrefugia characteristics on the changing area of the landscape occupied by each species.

Measuring importance across scenarios

We used a random forests algorithm (Breiman 2001) to assess the relative importance of these factors among the species functional groups analyzed. Random forests is a machine learning algorithm that builds many classification or regression trees to assess the hierarchy of factors (disturbance and microrefugia) affecting the response variable (range change). We treated range change (ratio of area change) as the dependent variable and disturbance regimes and microrefugia scenarios as explanatory variables and used variable importance as the metric to assess the strength of the relationship between each factor and range changes. Variable importance measures the difference in observed classification accuracy versus accuracy achieved by randomly permuting the variable. Greater differences imply greater importance of the variable in predicting the outcome of the regression. Calculations were performed using the randomForest package with default values of 500 trees (Liaw and Wiener 2002) in R version 3.1.1 (R Development Core Team 2014).

Climate change

We characterized a warming trend under climate change as a directional shift in environmental conditions with a correlated geographical and climatic gradient. That is, we simulated a displacement in the 'establishment niche' by progressively shifting P_est on the gridded landscape to a higher elevation during the climate change period (upper y-axis in the gridded landscape) (Fig. 1). We first simulated 100 years of dynamics without climate change to allow forest community self-sorting according to disturbance dynamics and microrefugia characteristics. We then simulated 100 years of climate change after this spin up period and regarded the beginning of climate change as time 0 for our analyses. As a result of warming, there was less available landscape for colonization by cold-adapted species at the end of the simulation, while warm adapted species increased their overall probability of establishment across the landscape. The rate at which the niche was displaced upwards was slightly non-linear, simulating patterns of accelerating twenty-first century climate change (see Electronic Supplementary Material 1 for detailed simulation specifications and parameters).

As a result of modeling climate change in this way, range dynamics were mainly driven by P_est. If a species was able to establish in a given cell, it aged until senescence occurred unless there was a

disturbance. At time 0, P_est and the initial species' distribution were aligned. That is, we considered species' distribution to be initially in equilibrium with climate, because climate gradients are the driver of P_est. Species P_est were drawn from a normal distribution of the environmental adaptation (described above) with a maximum of 0.2 and a minimum of 0.0001; these low values were used to establish realistic distributions of species under conditions of large amounts of seed rain occurring in our simulations due to a fairly high occupancy of the area.

Disturbance dynamics

Three disturbance regime scenarios were simulated: suppressed (0), high-frequency (H), low-frequency (L) (step 2 in Fig. 1). These were simulated with the Base Fire extension (He and Mladenoff 1999). Disturbance was spatially explicit with contagious spread; and the rate of spread was a probabilistic function of the time since last disturbance and the rate of fuel accumulation (He and Mladenoff 1999). Fire ignition probability or fire probability of occurrence spatial distribution did not vary as a function of altitude. Therefore, the same fire regime is applied to all the landscape under study. Disturbance initiation and frequency were stochastic, but varied across disturbance scenarios according to a user-specified probability of ignition. Disturbance size was also stochastic, with small disturbances more likely to occur than large disturbances, according to a log-normal distribution. Target minimum, mean, and maximum disturbance sizes were specified as parameters (see Electronic Supplementary Material 1). Multiple disturbance events often occurred in the same time step. Disturbances varied in severity according to time since last disturbance. Disturbance events were typically mixed severity; younger age cohorts were most susceptible to disturbance-related mortality, but cohort mortality was also a function of the disturbance severity.

We calibrated the disturbance extension to simulate scenarios that differed only according to disturbance frequency. Specifically, we targeted fire rotation periods of 100 and 200 years for the H and L scenario, respectively. This allowed us to investigate the effects of disturbance frequency without needing to consider other disturbance-regime characteristics, such as size or severity. For calibration, we used a manual optimization process, which involved stepping

through parameter ranges until the simulated frequency approximated our target (see Electronic Supplementary Material 1).

Climate microrefugia

Climate microrefugia were modeled as cells with stable high probability of establishment for a cold or a warm adapted species, thus they represented relatively small islands of climatically favorable habitat within regionally deteriorating conditions. By designating the establishment probability as the demographic factor that is stable in microrefugia, we emulated forest dynamics where establishment is the critical phase determining population and range dynamics. Microrefugia were mutually exclusive for the two climate adaptations: P_est for a warm microrefugia cell was 0.2 (maximum of establishment) for a warm adapted species and 0.0001 (minimum establishment) for a cold adapted species, and vice versa. It is important to note that in this simulation climate microrefugia only affect establishment, thus they should not be interpreted as disturbance refugia.

We developed several scenarios for microrefugia patterns to account for different spatial arrangements and levels of heterogeneity in our simplified landscape. We used the modified random cluster algorithm developed by Saura and Mart (2000) to produce thematic spatial patterns in a lattice for a given set of categories (e.g. warm climate microrefugia, cold climate microrefugia, no microrefugia; see Fig. 2). These patterns emulate different degrees of complexity and heterogeneity typically found in mountain regions. For instance, mountain ranges characterized by longer slope lengths are likely to display a higher aggregation of climatic microrefugia whereas mountain ranges characterized by shorter slope lengths (e.g. highly dissected landscapes) are characterized by higher spatial disaggregation of microrefugia.

We adjusted two parameters to simulate the aggregation pattern [p parameter in Saura and Mart (2000); selection probability] and the prevalence (or abundance) of a given category. We set two levels of aggregation: low ($p = 0.01$) and high ($p = 0.05$), and two levels of refugia prevalence: low (1 % of the landscape) and high (10 %). Therefore, a total of five combinations were available for each simulation: four microrefugia scenarios and one scenario without microrefugia. Because the output map of microrefugia

used random selection of cells, different output maps were obtained using the exact same parameters. For each combination of parameters, five replicate maps were generated and used in the simulations to account for stochastic variability.

Results

Disturbance and microrefugia interacted with species life history traits, producing different patterns of species range change (Fig. 2; see table of results in Electronic Supplementary Material 2). These effects were more consistent for cold-adapted species (the 'losers' under a global warming scenario) because of the loss of available habitat under the simulated environmental change. For warm-adapted species, results were more dependent on species traits.

Dynamics for the 'losers' [cold adapted species]

All scenarios predicted range reduction for cold adapted species (solid trend lines below the dotted

gray line in Fig. 2, and see Fig. 3a). Increased fire frequency resulted in greater mortality and decreased species area (Fig. 2). However, reduction in area due to increased disturbance frequency was lower for shade-intolerant species, as newly disturbed areas represented opportunities for recolonization (Fig. 2). Such opportunities were more accessible to long distance dispersers; thus, their reduction in area through climate change was lower (Fig. 3).

A greater prevalence of microrefugia tended to increase the overall total area of cold-adapted species. However, we observed a threshold response in the prevalence of microrefugia on species area: low prevalence of microrefugia resulted in lower species area than the scenario without any microrefugia (Fig. 2). More aggregated microrefugia reduced the total area of the shade tolerant species at the end of the simulation. However, for shade intolerant and short-dispersed species, a small increase was observed (Fig. 2).

Area lost accelerated through time in conjunction with the simulated rate of climate warming (Fig. 3a). In general, higher disturbance frequency generated greater area lost. However, under scenarios of
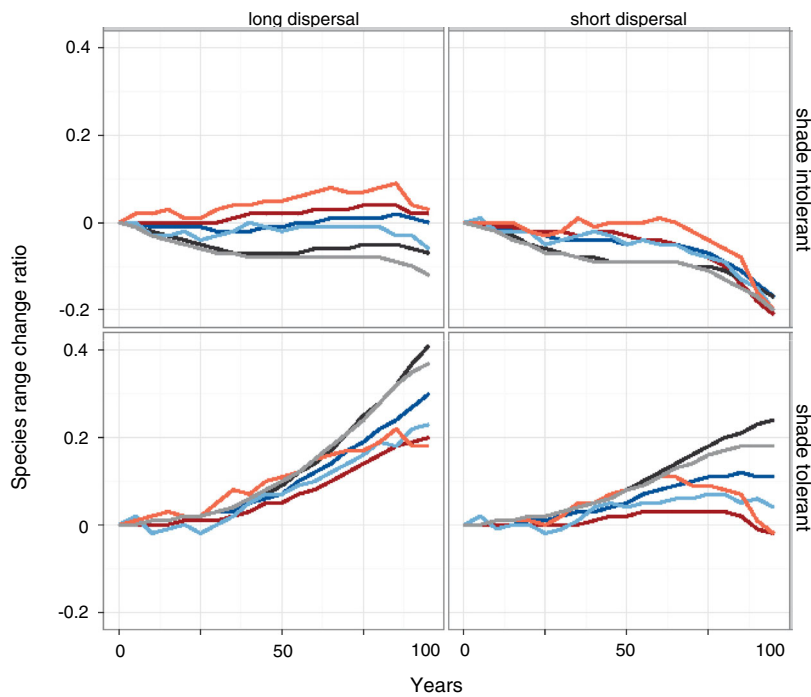

Fig. 2 Species range change after climate change, across species, disturbance and refugia scenarios. *Trend lines* in small *inset* graphs indicate the tendency of species range to increase or decrease across different intensities of microrefugia and disturbance frequency (scenarios). Overall trend is summarized by a symbol showing area of distribution change across scenarios. (+) increasing area with intensity of the scenario; (−) decreasing area with scenario (∼) non-monotonic trend. This results depict trends under different scenario changes. Scales are not comparable. See Fig. 3 and Electronic Supplementary Material 2 for actual range change ratios
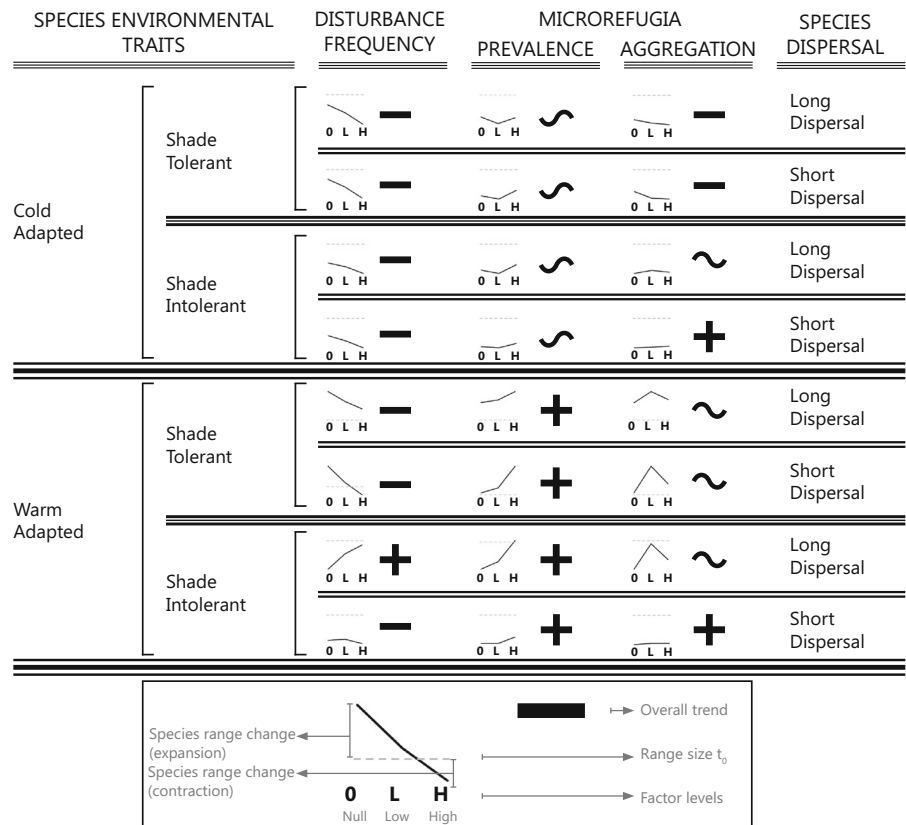
(a) Cold adapted species
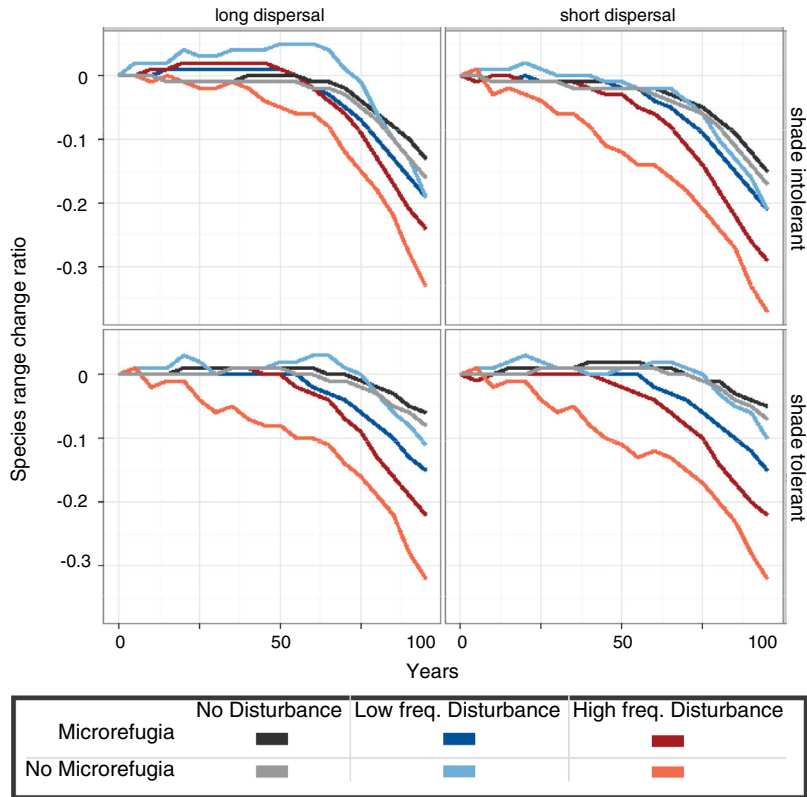
(b) Warm adapted species

◀ **Fig. 3** Species range change ratio through time during climate simulation; across species and disturbance and refugia scenarios for **a** cold adapted species **b** warm adapted species. Range change ratio is the ratio of area change relative to time 0 plotted for each time step and scenario. See Electronic Supplementary Material 2 for summarized tabular results

intermediate disturbance frequency, there were temporal windows of opportunity for regeneration, i.e., peaks of increase in the total area through time (light blue lines in Fig. 3a). This effect was more pronounced for shade intolerant species than for shade tolerant species. Under the no disturbance scenario, shade tolerant species increased slightly and shade intolerant species declined (black and gray lines, Fig. 3a). Microrefugia, regardless of spatial configuration and prevalence, produced a dual signal: area loss was diminished in high disturbance frequency scenarios but increased under low disturbance frequency scenario (Fig. 3a).

Dynamics for the 'winners' [warm adapted species]

Warm species range changes were highly dependent on the disturbance dynamics and available microrefugia (Figs. 2, 3b), with both increases and decreases in range size under different scenarios. Higher disturbance frequency was associated with decreases in total area except for the shade intolerant, long-dispersed species (Fig. 2). The null disturbance scenario yielded results that are coherent with a dynamics of a highly colonized forest landscape where a high degree of shading is the initial condition: a prominent increase of shade tolerant species adapted to such shading (Fig. 3b).

Microrefugia increased the overall range size relative to non-refugia scenarios. More microrefugia led to higher total range size of the warm-adapted species (Fig. 2). The degree to which microrefugia availability increased species area was, however, species specific. Some species required high frequency disturbance regimes to trigger increased distribution areas. These species were the shade intolerant-short dispersers and shade tolerant-long dispersers. For shade intolerant-short dispersers more microrefugia were needed for range expansion because this species was colonizing an already occupied landscape. This effect was important in our simulations because of our high degree of forest occupancy, and therefore a high degree of shade in our landscape. Consequently,

it implies for this species a high dependency on safe islands and disturbances because of its shade intolerance. For the shade tolerant-long dispersers, the cause of this low dose-response was the opposite; this species is a good colonizer of already occupied areas and therefore was less sensitive to changes in microrefugia availability.

Lower aggregation of microrefugia increased the range size of the warm-adapted species (Fig. 2). That is, low levels of aggregation facilitated colonization as more patches were available to be used by the species. As in the case of microrefugia prevalence, this effect was less pronounced in species with highly competitive traits for colonizing occupied sites (shade tolerant-long dispersers), or species lacking those traits (shade intolerant-short dispersers). In this latter case, the number of sites that could effectively be colonized was low regardless of their spatial distribution.

For species with a competitive advantage in either disturbance response (shade intolerant) or microrefugia colonization (long distance dispersers), the trade-offs were much clear cut: shade intolerant species increased their range size with higher disturbance frequency whereas the opposite occurred for shade tolerant species (Fig. 3b, top-left and bottom-right panels, respectively). Interestingly, species range change for shade intolerant-long dispersal species was dependent on the interaction between microrefugia and disturbance regimes. In the case of low frequency disturbance, shade intolerant species slightly increased their range, but only if microrefugia are available; otherwise, the species range size declined (Fig. 3b, top-left panel, dark blue vs. light blue lines). Conceptually, this implies that the likely outcome of range shifts (shrinking versus expanding) may be dependent on key dispersal traits when disturbance regimes do not offer enough opportunities for colonization.

In general, the availability of microrefugia tended to increase range size but our results highlight threshold interactions with disturbances. In the case of very frequent disturbance, having microrefugia—and thus heterogeneity—decreases the chances of colonizing 'safe islands' for establishment.

Factor importance in simulations

The most important factor determining species range change was disturbance, followed by microrefugia prevalence and aggregation patterns for the majority

Table 1 Hierarchy of importance of disturbance and microrefugia in species range change for each species analyzed

Species climate adaptation	Species light tolerance	Species dispersal	Disturbance regimes	Microrefugia prevalence	Microrefugia aggregation
Warm	Tolerant	Long	2.79 (0.07)	0.70 (0.02)	0.42 (0.01)
Warm	Tolerant	Short	2.01 (0.05)	0.50 (0.01)	0.36 (0.01)
Warm	Intolerant	Long	0.13 (0.00)	0.24 (0.01)	0.02 (0.00)
Warm	Intolerant	Short	0.31 (0.01)	0.79 (0.02)	0.27 (0.01)
Cold	Tolerant	Long	1.22 (0.02)	0.06 (0.00)	0.03 (0.00)
Cold	Tolerant	Short	1.03 (0.02)	0.12 (0.00)	0.03 (0.00)
Cold	Intolerant	Long	0.82 (0.02)	0.11 (0.00)	0.05 (0.00)
Cold	Intolerant	Short	0.51 (0.01)	0.36 (0.01)	0.03 (0.00)
All species			1.10 (0.84)	0.36 (0.26)	0.15 (0.16)

Importance measured as a mean decrease in Gini index. Number in parentheses indicate standard deviation of 100 iteration of the random forest model

of species (Table 1). For the two warm-adapted and shade intolerant species, however, the availability of habitat for colonization had the greatest effect on range change. In this case, the variable importance for prevalence was slightly higher than disturbance (although this difference was much smaller than in the other cases where disturbance was the most important variable). This suggests that for species with these traits, both factors were equally important.

Discussion

The interaction among species traits, disturbance dynamics, and microrefugia largely affected the pace as well as the availability of species to track climate change. Disturbance provided both opportunities for colonization and accelerated range shifts. Climate microrefugia, in turn, provided both persistence as well stepping stones for species migrations. Our simulations demonstrate a wide array of range responses resulting from the interactions among these factors and highlight the many possible outcomes in response to climate change when landscape heterogeneity and disturbance are taken into account, which we discuss below.

The multiple roles of disturbance

Disturbance mediates forest dynamics by removing vegetation and altering competition for resources. This in turn provides advantages and disadvantages relative

to species' traits, the location of disturbance in relation to other species, and other disturbances in space and time (Denslow 1980; Pickett 1985). Our simulations demonstrated that disturbance can potentially play a key role in mediating range changes through its effect on colonization.

In some cases disturbances expedited range contractions at a non-linear rate rather than changing the overall trend of the range change. This effect has also been predicted for tree species range change in the eastern US, considering harvesting as a disturbance (Vanderwel and Purves 2014) and in Europe (Sykes and Prentice 1996). However, our experiment also showed how the lagged response of species to deteriorating conditions in situ combined with the inability of another species to colonize new suitable habitat (owing to poor competitive and/or dispersal ability) can facilitate persistence (Davis 1989). Warm-adapted species, which were expected to have an expanding climatic niche, may have difficulty colonizing environments that are already occupied, that otherwise might be made available through disturbance. This highlights vegetation's lagged responses (Scheller and Mladenoff 2008; Kuussaari et al. 2009; Bertrand et al. 2011) as a barrier to other species colonization. Therefore the role of disturbance on range shifts is crucial.

Although the species in our simulations were modeled to have a uniform susceptibility to mortality from disturbance, most landscapes consist of species adapted to specific disturbance regimes. Therefore, if disturbance regimes are altered beyond their natural

range of variability, the role of disturbance in species' range changes may be accelerated by mortality and recruitment dynamics acting synergistically. For example, disturbance-sensitive species may be extirpated from an area due to large-scale mortality resulting from increased disturbance frequency or size (Swab et al. 2012), or recurrent drought events may drive mortality of some species and facilitate recruitment of others (Galiano et al. 2010). On the other hand, disturbances may act similarly to microrefugia by providing holdouts or stepping stones (Hannah et al. 2014), enhancing the ability of species to migrate to more suitable conditions. Disturbance provides successional opportunities for colonization in otherwise occupied space, e.g. a temporal regeneration niche or refugia (Grubb 1977; Long et al. 1998; Mackey 2002).

Assessing and predicting general effects of disturbance on species' distributions is difficult, in part because of the correlation between climate and disturbances regimes (climate related disturbance such as fire, drought, etc.). To date, correlative species' distribution models have shown mixed results regarding the role of disturbance. In some cases, species' distributions may be better predicted based on their disturbance-response mechanism (Scheller and Mladenoff 2008; Syphard and Franklin 2010) whereas other studies found little model improvement to justify the explicit use of disturbance as a predictor variable in statistical distribution models (Crimmins et al. 2014). However, we expect future disturbance regimes in many regions to increasingly blur the relationship between species' distribution and climate (Cassini 2011), especially as human-generated disturbances may become more prominent in the Anthropocene (Steffen et al. 2007). Not only species' distributions but also disturbance regimes are affected by multiple human-generated disturbances. For instance, a climate-related disturbance, such as wildfire, can be more profoundly affected by human activities or land uses, than by climate (Syphard et al. 2009; Keeley and Syphard in press).

Climate microrefugia

Microrefugia are often found in heterogeneous areas where environmental variation is large over short distances. In our simulations, increasing the microrefugia area produced a similar effect by introducing local areas of both high and low probability of establishment. The prevalence of climate microrefugia was a more important factor for range change than spatial aggregation (Table 1). However, microrefugia did not reverse the overall trend for cold adapted-high elevation species that were parameterized to lose habitat under global warming. Mountains can be reservoirs of diversity during unfavorable conditions but can also create barriers to migration for species with low dispersal capacities as well as barriers to disturbances. Such differences in species ability to colonize microrefugia may explain genetic differences among tree populations (McLachlan et al. 2005) and highlights that microrefugia will contain a subset of the total pool of species within a region (Mosblech et al. 2011).

For the majority of species, climate microrefugia scenarios affected range change to a lesser extent than disturbance regimes. One possible explanation is that microrefugia affected a smaller area of the landscape than disturbance but we emphasize that it was the array of interactions that motivated our study (See boxplots and interactions among factors described in Electronic Supplementary Material 3).

Note, however, that the potential correlation between climate refugia and disturbance refugia was not simulated. Indeed, a topographically mediated climate that promotes establishment can also support longer disturbance return intervals. For instance, the same complex topography that promotes refugia for species establishment may also reduce the probability of wildfire (Taylor and Skinner 1998; Beaty et al. 2001; Dillon et al. 2011). Therefore, portions of the landscape that resist disturbance could also further enhance species persistence. All in all, it is likely that our simulations underestimated the importance of microrefugia in promoting persistence if the disturbance is strongly correlated to the same climate variation that produces climate refugia. However, incorporating such behavior would not qualitatively change the results found here. In our landscape, microrefugia are modeled as having a very high probability of species establishment, also implying very high regeneration after a disturbance event. Moreover, the prevalence of our species in the landscape is relatively high—implying widespread seed availability—and the disturbance simulated did not tend to kill all the cohorts. In addition, the use of species presence, as opposed to abundance or cohort age, as our response variable makes our results less

sensitive to such interactions. Also, it is likely that climatic extreme events may blur the relationship between disturbance—and its properties—and topography (Thompson and Spies 2010; Dillon et al. 2011). However, we recognize that the role of disturbance refugia can have a strong effect on species persistence (Schwilk and Keeley 2006).

Finally, trade-offs between species traits and microrefugia spatial arrangement are important to understand. Such interactions have already been documented elsewhere. For instance, Bhagwat and Willis (2008) used fossil and genetic data in refugial localities in Europe, and found that large seeded trees occurred only in certain southern refugia whereas wind-dispersed species were more fully distributed across refugia. Potts et al. (2013) found evidence for interactions between dispersal and landscape complexity, as drainage basins could become barriers to gene flow for dominant tree species in South Africa dependent upon seed dispersal traits.

Delimitations of this study

Models simplify reality. The forest community represented in our simulations was intentionally simplified; indeed the relative orthogonal frequency of species traits depends in the location of the analysis but species rarely possess perfectly orthogonal trait combinations. For this reason, there is debate as to whether traits are actually meaningful to range shifts (Angert et al. 2011). Nevertheless, our eight species represent the range of strategies typically found in mountainous temperate forests. Also, climate change may cause species' distributions to shift in multiple directions (VanDerWal et al. 2012) rather than a unidirectional niche shift simulated in this study. Furthermore, leading and trailing ranges within the same species may exhibit different *bioclimatic velocities* and range patchiness in space and time (Serra-Diaz et al. 2014). Our analysis emphasizes that even assuming such unidirectional responses—higher altitudinal migration—species' distributions may still reflect different distributional responses due to interactions between species traits, disturbance regimes, and microrefugia.

Our simulations were strongly focused on the effects of microclimates and microrefugia on species establishment, although we acknowledge the potential pervasive effects of warming on mortality. Therefore, our simulations may have underestimated the capacity

of shade intolerant species to colonize new sites as trees experience mortality due to drought and associated disturbances (e.g. insect outbreaks). Also, persistence of cold adapted species could be shortened if climate change did also affect mortality rates as well as establishment. We believe that our results are valuable to the extent that the capacity of adults to survive under varying environmental conditions is generally larger than juvenile stages (Harper et al. 1977; Dobrowski 2011; Bell et al. 2014). Therefore, focusing on the more sensitive juvenile stage may be key to understanding species distributional changes in the next century (Grubb 1977; Harper et al. 1977; Zhu et al. 2012).

Another simplification in this study was that our experiment only considered the effect of disturbance frequency whereas several other properties of disturbances—spatial distribution, severity, size, species-specific responses, etc.—may also be key to understand species' distributions (Dale et al. 2001) and the relative importance of disturbance may be context dependent: a densely forested landscape in our case. Lastly, disturbance did not vary as a function of time in our simulations although we acknowledge the wide range of feedbacks between disturbances and climate change (Ayres and Lombardero 2000). We argue that these simplifications do not compromise the realism and insights of this study that purposefully limited complexity to highlight how disturbance and climate refugia affect species' distributions under a changing climate.

Towards a better understanding of successional dynamics in the face of global change

Our modeling experiment serves as a foundation for future research that incorporates greater complexity and realism into simulated range dynamics, including more species, with greater heterogeneity of life history and disturbance response traits, spatially and temporally heterogeneous disturbance regimes, and microrefugia. Our results emphasize that species traits influence but may not entirely explain species range change (Angert et al. 2011) and that an understanding community dynamics is also required. This highlights the need to simulate non-deterministic successional dynamics in order to understand tree species range dynamics under rapid climate change. Species favored by climate change may be dependent on other processes (dispersal, competition and disturbance),

as well as patterns of suitable habitat, to successfully colonize new ranges. We suggest moving beyond the vision of disturbance as a simple range eroding process to a framework that views landscape heterogeneities and disturbance as important features for range changes. Future research must address the interactions between species traits, climatic dynamics and heterogeneity and disturbances in order to understand species range change as an emergent property of interacting dynamics.

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