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Modelling effects of habitat fragmentation on the ability of trees to respond to climatic warming

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The ability of trees to migrate in response to climatic warming was simulated under various conditions of habitat availability. The model uses Holocene tree migration rates to approximate maximum migration rates in a forested landscape. Habitat availability and local population size was varied systematically under two dispersal and colonization models. These dispersal models varied in the likelihood of long-distance dispersal events. The first model used a negative exponential function that severely limited the probability of long-distance dispersal. The results of this model indicate that migration rate could decline an order of magnitude where the habitat availability is reduced from 80 to 20% of the matrix. The second model, using an inverse power function, carried a higher probability of long-distance dispersal events. The results from this model predict relatively small declines in migration rates when habitat availability is reduced to 50% of the simulation matrix. Below 50% habitat availability, mean migration rate was similar to the negative exponential model. These results predict a failure of many trees to respond to future climatic change through range expansion.

Keywords: tree migration; deforestation; Holocene; simulation model; global warming

Introduction

An important ecological response to global warming will be shifts in geographical distributions of plants (Davis, 1989; Graham and Grimm, 1990; Huntley, 1991; Davis and Zabinski, 1992). Current predictions cite that trees will need to shift approximately 100km northward for each 1°C of warming (Davis, 1989; Melillo *et al.*, 1990). Climatic parameters that describe current species ranges are predicted to shift more than 500km northward during the next century (Davis and Zabinski, 1992). In contrast, observations of Holocene tree range expansion rates, which I will henceforth refer to as 'migration rates', fall far below those required to keep pace with predicted future warming trends. Holocene tree migration rates averaged 10–45km per century (Davis, 1981; Huntley and Birks, 1983), with a maximum rate of 200km per century (Ritchie and MacDonald, 1986). These Holocene migration rates are believed to approximate maximum migration rates for most trees (Huntley, 1989, 1991). Evidence that Holocene migration rates approximate maximum migration rates comes from two sources. First, detailed historical vegetation studies have detected occasional migration lags in species response to climatic change (Davis, 1984; Davis *et al.*, 1986; Pennington, 1986). Second, the relative constancy of maximum migration rates of individual taxa between geographical areas suggests that these migration rates were not limited by rate of climate change, which varied across geographical regions, but by dispersal and colonization (Huntley, 1989). The conclusion drawn from these historical observations is that future plant migration

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rates will lag behind climatic warming (Davis, 1989; Overpeck *et al.*, 1991; Huntley, 1991).

In this paper a simulation model is used to propose that Holocene migration rates, alone, are not the appropriate model for predicting migration rates in response to human-induced climatic warming. Habitat loss is likely to further slow migration response of most species. Deforestation and habitat alteration of modern landscapes may create new barriers for the migration of trees (Dunn *et al.*, 1991; Peters, 1991). The importance of habitat loss on species migration and subsequent biodiversity remains an open question.

The ecological and epidemiological literatures present several models for random dispersal of propagules resulting in range expansions (e.g. Skellam, 1951; Gregory, 1968; Fitt and McCartney, 1986; Okubo and Levin, 1989). Although not explicitly addressed, one can deduce from these models that, under a model of random dispersal, reducing the availability of suitable habitat reduces a species capability for range expansions. However, the magnitude of this factor has not been considered directly.

Similarly, Carter and Prince (1981, 1988) propose that species may be limited geographically by the frequency of suitable habitats. Carter and Prince (1988) predict that, although species may be common locally within a suitable habitat, the probability of habitat colonization is very low when patches of suitable habitat are rare. Carter and Prince claim that near a species distribution limit population extinction rates equal new site colonization rates because suitable habitat is rare. As the probability of colonization approaches that of local extinction, a species ceases to expand its range. Thus, Carter and Prince (1988) provide a possible explanation for why species ecological range limits may not be congruent with physiological range limits, and why a direct link between climate and plant distribution is often elusive.

This paper describes a simulation model that varies local population size and habitat availability to predict migration rates for species. Parameters of the model are based on trees of the mesic northern mixed-hardwood forests of eastern-North America. The dispersal of propagules in this model is random with respect to habitat. Thus, the model is most appropriately applied to trees with wind-dispersed seeds, although random dispersal models are considered analogs for many types of dispersal (Skellam, 1951). The simulation model is presented to bracket realistic predictions of tree species migration response rates to climatic warming under conditions of reduced habitat availability. These results are important because they explicitly quantify the impact of habitat loss on the ability of species to migrate.

The general predictions of this model should be applicable to a broad range of plant species. This is an important consideration given that historical observations upon which to base a simulation model do not exist for most animal pollinated plants. The specific predictions of the model are based on three important assumptions:

(i) mean temperatures will increase 4–6°C in eastern-North America during the next century (see Mitchell *et al.* (1990) for review);

(ii) equilibrium range shifts will be approximately 100km per 1°C of warming (Melillo *et al.*, 1990; Davis and Zabinski, 1992);

(iii) tree migration rates during the Holocence approximate maximum migration rates (Davis, 1981; 1989; Huntley, 1989, 1991).

Methods

This single species model was designed to focus on the issue of migration in the absence of all other ecological factors. The model consists of a 30km by 400km matrix of $4km^2$ habitat cells through which a hypothetical tree species was allowed to migrate. The minimum size of actual forest fragments is, of course, smaller. This cell size was chosen for tractability of the computer stimulation. Migration across the entire length of the matrix is within the range of expected climate-induced distribution shifts under doubled CO_2 for the eastern-North America (Mitchell *et al.*, 1990; Peters, 1991; Davis and Zabinski, 1992).

Each simulation was run for 500 years. This interval was divided into ten generations of 50 years, a typical generation time for trees of the mesic northern mixed-hardwood forest (Loehle, 1987). A simulation is begun by establishing a discrete species front in the southern 20km of the matrix; the remainder of the matrix was unoccupied by the migrating species. A discrete range edge is modeled to mimic the distribution terminus of species typically limited by winter minimum temperatures or growing degree days (Little Jr, 1971; Woodward, 1987).

This stimulation model excludes interspecific interactions. The dispersal function combines properties of dispersal, germination, and survival to maturation over the course of each generation. All propagules that successfully 'land' in an unoccupied site become mature reproducing adults by the next generation. Consequently, 'unoccupied' cells are only unoccupied with respect to the migrating species. Since the model is designed for trees, one can think of suitable habitat as forested land and unsuitable habitat as nonforest land.

Analyses were made using two common types of dispersal functions (Okubo and Levin, 1989). The first, a negative exponential function (Frampton *et al.*, 1942; Harper, 1977), has a much lower likelihood of long-distance dispersal events than the second, an inverse power function (Gregory, 1968). Empirical tests fitting observations of dispersal to these models do not indicate a preference between them (Gregory, 1968; Fitt and McCartney, 1986; McCartney and Bainbridge, 1984; Okubo and Levin, 1989).

These dispersal functions were chosen to mimic two types of seed dispersal by wind. The negative exponential function used in model 1 is characterized by a very low probability of colonization of outlying cells and approximates the migration pattern of species with heavy wind-dispersed seeds such as maple (*Acer* spp.). Alternatively, the inverse power function represents dispersal of species with light wind-dispersed seeds, such as hemlock (*Tsuga canadensis*). The current distribution of hemlock includes numerous outliers beyond the contiguous limit of the species. While these outliers represent past long-distance dispersal events (Calcote, 1986), the frequency of outlier establishment is unknown.

The dispersal functions were used to calculate the probability that propagules from one occupied cell successfully colonized an unoccupied cell. Exponential reduction in seedling establishment with increasing distance from a seed source is a commonly observed pattern for trees (Harper, 1977; Johnson, 1988; Johnson *et al.*, 1981). Model 1 used a negative exponential function for the probability of colonization across distance:

$$P_{i,t} = \sum_{j=1}^{n} F_{j,t} \times C/2^{D_{i,j}} \qquad (1)$$

while model 2 used an inverse power function of the distance between sites to determine colonization probability:

$$P_{i,t} = \sum_{j=1}^{n} F_{j,t} \times C/D_{i,j}^{3} \tag{2}$$

In both models, $P_{i,t}$ is the probability of site 'i' being colonized at time 't'; $F_{j,t}$ is a scalar used to adjust for species abundance at site 'j' at time 't'; $D_{i,j}$ is the distance between the unoccupied site 'i' and the occupied site 'j'; and C is a constant used to calibrate the migration rate. The purpose of this constant was to set simulation migration rates to match empirical observations of Holocene migration rates under conditions described below.

Simulations were repeated varying maximum tree abundance (F_{max}) and habitat availability. To account for the fact that abundance varies among species, five levels of maximum tree abundance were used. The values (0.1, 0.3, 0.5, 0.7 and 0.9) represent the maximum frequency that the migrating species may attain within a habitat. The values were selected to represent a range from uncommon to very abundant species. The proportion of cells defined as habitat suitable for colonization was varied in 0.1 increments from 0.1 to 0.9. Cells with suitable habitat were randomly chosen prior to each run from within, as well as beyond, the region of initially occupied cells.

The constants (C) for each model were selected, through test runs, to achieve a migration rate between 30km and 50km per century when 80% of sites were available for colonization and F_{max} was equal to 0.5. These values were chosen to represent a moderately common tree of the dominant forest-type in a largely forested landscape, analogous to maple or hemlock moving into the Midwest during the Holocene (Davis, 1981; Davis *et al.*, 1986).

Five replicate simulations were conducted for each level of habitat abundance and maximum species frequently for both dispersal functions, resulting in 450 simulation runs. At each time step (generation) of each simulation run I calculated the probability for each unoccupied cell to become occupied. A random number, between 0 and 1.0, was selected for each unoccupied cell and compared to the colonization probability to determine whether the cell became colonized. Newly colonized sites were defined to carry a species frequency ($F_{j,t}$) equal to 6% of the maximum. The species frequency of a cell was doubled in each of the subsequent four generations to reach the maximum frequency for that run. After four generations $F_{j,t}$ became fixed at F_{max} for the remainder of the simulation run. This simple within-site population growth convention roughly approximates logistic population growth to carrying capacity. Colonized sites contributed to the probability of further site colonization in all subsequent generations.

In initial runs I tried various methods for detecting the species front. These trials attempted to approximate a realistic detection threshold for species range limits. Differing the sensitivity of range limit detection altered migration rates, and hence changed the value of the constant needed to calibrate the model under 'natural' conditions. These various conventions for defining the species range limit, however, consistently affected simulations differing in habitat availability and maximum species frequency. Thus, the exact nature of convention chosen for species range limit detection does not substantually alter the results. For the final version I defined the species' front as the upper (northernmost) five consecutive rows of cells where 50% or more of the suitable habitat was occupied.

This simulation model contains several simplifying characteristics. Firstly, local extinction is not incorporated into the model. Local extinction events would lower migration rates and create a threshold of habitat abundance below which species will not expand (Carter and Prince, 1981, 1988). Secondly, colonization is equally likely in all directions from an occupied site. Thirdly, colonization rate is assumed to be constant across varying habitat patchiness. In reality, however, isolated forest fragments can experience higher wind speeds, resulting in an increased frequency of long-distance dispersal of wind-dispersed seed (Johnson *et al.*, 1981).

Fourthly, no distinctions are made among suitable habitats of differing quality, i.e., matrix cells represent habitat that is suitable or not suitable. Although most estimates of deforestation do not assess remaining habitat quality (Curtis, 1856; Dunn *et al.*, 1991; Iverson *et al.*, 1991), such differences in habitat quality may affect colonization ability (Dunn *et al.*, 1991). Incorporating suitable habitat cells of lesser quality would reduce the predictions of migration rates for any given level of habitat abundance. Finally, a finite range shift is modelled. The model is established to simulate range changes precipitated by the magnitude of warming predicted for eastern North America (Mitchell *et al.*, 1990). By limiting the matrix size to 400km I create a finite limit to the extent of migration and prevent migration beyond this boundary. This characteristic, as discussed below, only affects the results when suitable habitat is abundant and maximum species frequently is high.

Results

For each set of conditions 500 years of migration with four measures are summarized: mean migration rate, mean front position after 500 years, mean maximum extent of colonized cells, and mean percentage of suitable habitat filled. These four measurements are strongly correlated with the per generation migration rate ($R^2 > 0.99$ in all cases). Only the mean per generation migration rate expressed as km per century are presented. For model conditions where suitable habitat is abundant (90% of cells) and maximum species frequency is high ($F_{\max} = 0.7$ and 0.9) migration rates were high and the habitat matrix became saturated by the migrating species prior to the end of the run. Under these simulation conditions the final two generations of each simulation run are eliminated from consideration in calculating the mean per generation migration rate.

Under both dispersal functions several moderately high levels of species frequencies and habitat suitability approximate historically observed migration rates (Fig. 1). Slight differences between models arise from the fact that the target migration rate, at 80% habitat availability and $F_{\max}$ equals 0.5, was slightly higher (52km/ century) for model 2, the inverse power function, than for model 1, the negative exponential function (30km/ century). Despite these differences, all levels of species' abundance result in migration rates that fall well below historically observed migration rates at low levels of habitat availability. Migration rates varied between 0.5 and 13km/century when less than 30% of sites are available for colonization. Likewise, rare species (less than 0.3) never attain high rates of migration even when suitable habitat is abundant (Fig. 1).

The two models varied slightly in migration rate response with respect to habitat availability (Fig. 1). At each species abundance level the negative exponential model resulted in a steady decline in mean migration rates with declining habitat availability. This results in an order of magnitude decline in migration between 'natural' conditions

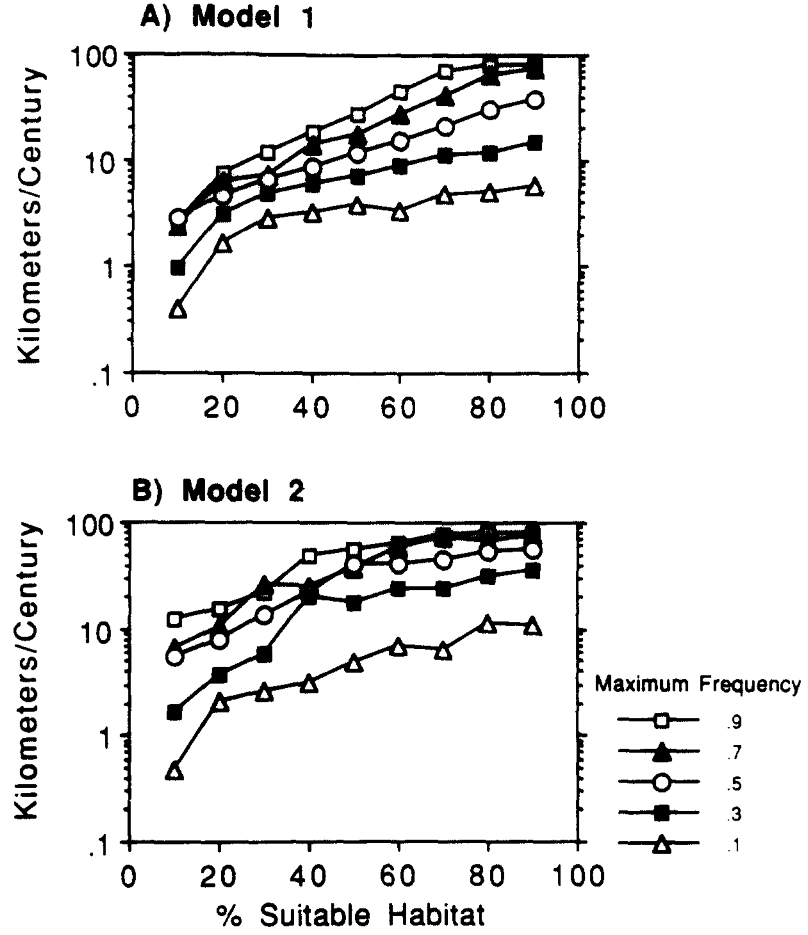

Figure 1. Mean tree migration rates under various combinations of suitable habitat abundance and maximum species frequency within habitat. Each point represents the mean of 50 observations, five replicate runs of ten generations each. A) Model 1: the colonization probability is related to distance by a negative exponential function, B) Model 2: colonization probability is a function of the inverse of the cubed distance between sites.

(80% forested) and realistic levels of habitat abundance for agricultural regions (< 30% forested).

For the inverse power function, there is a slight decline in migration rate down to 50% habitat availability (Fig. 1). At 40% habitat availability and below the mean migration rate falls dramatically for all levels of species frequency (Fig. 1). Mean migration rates for the inverse power function are decreased by an order of magnitude when habitat availability is reduced to 20%.

To characterize the difference between the two dispersal functions I plotted the probability that an individual occupied cell with a species frequency of 0.5 successfully colonizes an unoccupied cell at varying distances (Fig. 2). To illustrate how these differences in colonization probability affect the model results I measured the mean

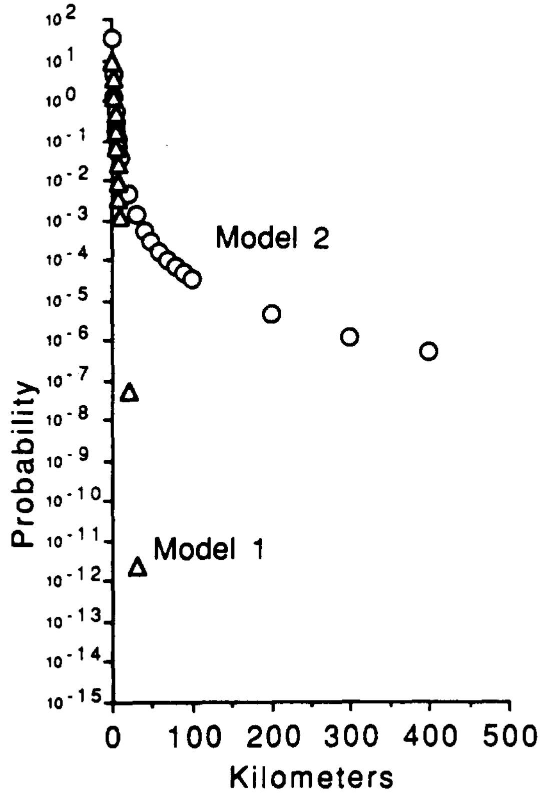

Figure 2. The two colonization probability functions plotted against distance. Y-values represent the probability of an occupied cell emitting a propagule that colonizes an unoccupied cell at various distances (X).

maximum distance between the northernmost occurrence and the species front for each run. For a common species ($F_{max} = 0.5$) with abundant suitable habitat (0.7) the mean maximum distance between the species front and the northernmost occurrence was 28km for the negative exponential function (model 1), and 197km for the inverse power function (model 2). Thus, these models varied substantially in the frequency of long distance dispersal.

In every simulation run using the inverse power dispersal function (model 2) where the availability of suitable habitat was high (> 40%) I witnessed the colonization of a cell upwards of 100km beyond the range limit of the migrating species. This inverse power function model undoubtedly over-estimates the true probability of long-distance establishment. However, this characteristic is desirable since it allowed the model to assess whether the ability to disperse long distances can compensate in a fragmented habitat.

Discussion

It can be no surprise that both habitat loss and a reduction of species abundance reduce migration rates. To a large degree, these factors are intuitively obvious. The fewer trees in the environment, represented either by the number of occupied habitats or the abundance within habitats, the fewer seeds produced. Further, fewer suitable habitat results in a lower probability that seeds will land in a suitable site and successfully recruit. The real interest of this simulation comes from studying the magnitude of these effects.

This model uses widely accepted functions that describe dispersal and colonization in plants. These dispersal and colonization functions are grounded in empirical observations (Gregory, 1968; Fitt and McCartney, 1986; McCartney and Bainbridge, 1984; Okubo and Levin, 1989). The simulation model was intentionally designed to favour migration response in several ways. For instance, the inability of occupied cells to experience a population reduction or local extinction increases migration response. In addition, the designation of all suitable habitat as equally suitable over-estimates the quality of many forest fragments with respect to colonization. Finally, by establishing a constant colonization probability function this simulation models a step-change in climate during the first year of the simulation, thereby maximizing a species' ability to respond to climate change.

Despite creating a conservative model, the decline in migration rate with habitat loss is remarkably high. Further, the ability for long distance dispersal does not adequately compensate for the effects of habitat loss or population reduction. The observation that the two dispersal and colonization probability functions derive similar results, despite greatly differing underlying probabilities of outlier establishment, indicates that these results are robust over changes in the spatial arrangement of suitable habitat.

These results accentuate prior predictions of the inability of plants to geographically respond to global warming (Davis, 1989). Many forested regions of the temperate world have been largely deforested, or significantly disturbed. Regional estimates of the amount of forest habitat remaining on the modern landscape of eastern-North America vary from 5% to 80% of presettlement levels with most agricultural areas near the low end of the scale (Curtis, 1956; Dunn *et al.*, 1991; Iverson *et al.*, 1991). Even regions that are largely forested at the present time, such as the north-eastern USA, have been logged and are now second growth forests of uneven quality. It is not known how suitable many of these managed second growth forests are for colonization by slow-growing, shade-tolerant trees.

I predict that migration rates on the modern landscape will be significantly slower than rates observed during the Holocene. Many species may not respond to warming during the next century in any detectable manner. For instance, observations of Holocene migration rates fall approximately one order of magnitude below predictions of future migration rates required to keep pace with warming (Davis, 1989). In regions where less than 30% of the landscape is suitable for colonization this model predicts future migration rates an order of magnitude slower than Holocene observations (Fig. 3).

Beyond illustrating how inherent migration rates could differ among common versus rare species, this simulation model summarizes how a reduction of frequency within stands in the modern environment can inhibit migration. Hemlock (*Tsuga canadensis*) illustrates this particular problem. Increased deer herbivory of young hemlock has severely reduced hemlock recruitment in parts of its range (Anderson and Loucks, 1979; Alverson *et al.*, 1988). With a reduced number of habitats as a result of logging, and reduced within-stand abundance, hemlock is likely to be slow to respond to climatic change.

This model predicts a substantial decrease in the migration rates of trees in response to

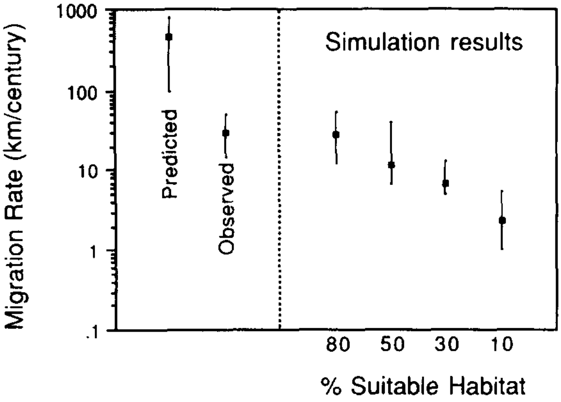

Figure 3. A schematic diagram of species' migration rates. The 'predicted' range indicates migration rates needed to maintain a distribution in equilibrium with current climatic parameters that describe distribution based on predictions of future climate change. The 'observed' range are average rates of Holocene tree migrations based on palynological data. Square symbols in the predicted and observed ranges denote means. The simulation results indicate the range of migration rates predicted, using either dispersal and colonization function, for a moderately common ($F_{max} = 0.3, 0.5, 0.7$) wind-dispersed tree. Square symbols in the simulation results indicate the predicted migration response for a common species ($F_{max} = 0.5$) using the negative exponential dispersal and colonization function.

climatic warming. An additional problem is that most forest fragments on the modern landscape are relatively young, second growth forests. These younger forest fragments represent a different colonization resource than mature forest. Holocene migration rates varied between species (Davis, 1981; Huntley and Birks, 1983). It seems likely that these differences will be accentuated in the future as a result of differential abilities among species to invade second growth forests. We need more empirical information on species colonization in sites of differing stand age and quality.

We should also expect differences in the patterns of species migration response to future climate change. Species' response to climatic change during the Holocene was individualistic with respect to pattern (Davis, 1981; Huntley and Birks, 1983). Forest fragmentation is not uniform. The results of this model suggest that future species migrations are likely to be channeled through regions where the landscape has remained forested or become reforested, such as the Appalachian Mountains.

The problem with gauging species level response to climatic warming is that CO_2 enhancement precipitates numerous direct physiological responses in plants (Melillo *et al.*, 1990). Many of these physiological changes may affect the need for some species to expand northward. Thus, it will be difficult to determine whether a lack of migration response is the result of physiological acclimation to modified climate or low dispersal probability.

With respect to biodiversity the models presented here reiterate an important observation made earlier (Davis, 1989). Species with geographically restricted ranges, such as narrow endemics, could be especially threatened by climatic warming. These species are often restricted to habitat islands, are uncommon within their habitats, or are specialists on uncommon habitats. As such, the inherent probability of dispersing propagules to other appropriate habitats is low. These types of species will be at risk of extinction if climate becomes unsuitable within a species' distribution and it is unable to migrate. Further, preserves designed to protect species may no longer afford protection as climate changes.

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