

LETTER

Antagonistic effects of seed dispersal and herbivory on plant migration

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Abstract

The two factors that determine plant migration rates – seed dispersal and population growth – are generally treated independently, despite the fact that many animals simultaneously enhance plant migration rate via seed dispersal, and decrease it via negative effects of herbivory on population growth. Using extensive empirical data, we modelled the antagonistic effects of seed dispersal and herbivory by white-tailed deer on potential migration rates of *Trillium grandiflorum*, a forest herb in eastern North America. This novel antagonistic interaction is illustrated by maximum migration rates occurring at intermediate, but low herbivory (< 15%). Assuming herbivory < 20% and favourable conditions for population growth during post-glacial migration, seed dispersal by deer can explain rates of migration achieved in the past, in contrast to previous models of forest herb migration. However, relatively unfavourable conditions for population growth and increasingly intense herbivory by deer may compromise plant migration in the face of present and future climate change.

Keywords

Deer, dispersal, forest herb, glaciation, herbivory, Holocene, migration, population growth, *Trillium grandiflorum*.

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INTRODUCTION

The most common biotic response to climate change is migration of species ranges (Jackson & Overpeck 2000). The degree to which a species can track favourable climatic conditions depends on its potential migration rate, which, in turn, depends on two main factors: the species' capacity for dispersal, and its rate of population growth in newly established populations (Clark *et al.* 2003; Higgins *et al.* 2003). These two aspects of a species' biology are generally treated independently in efforts to model potential migration rates in the face of climate change (e.g. Cain *et al.* 1998; Clark *et al.* 2003). However, for many species, conditions that favor increased dispersal (thereby enhancing migration rate) may also decrease local population growth (thereby reducing migration rate). For example, a variety of vertebrate and invertebrate animals are more likely to disperse when local conditions for population growth are relatively poor (Baker 1978). For plants, a particular animal that disperses seeds may also decrease population growth via seed predation or herbivory. Rodents and birds, for example, both disperse and destroy seeds of many plants

(van der Pijl 1982). Large herbivores disperse seeds of a wide range of plant species (e.g. Myers *et al.* 2004), but may also have severely negative population-level effects via herbivory (e.g. Knight 2004). In such cases we cannot simply ask how increasing dispersal influences migration rate, because dispersal cannot realistically increase without concomitant increases in seed predation or herbivory. Here, we combine extensive data sets on both seed dispersal (Vellend *et al.* 2003) and herbivory (Knight 2003, 2004) by white-tailed deer on *Trillium grandiflorum* (Michx.) Salisb., a forest understory herb in eastern North America, to model the net effect of deer on the potential rate of plant migration.

Seeds of many temperate forest herbs, including *T. grandiflorum*, are dispersed primarily by ants, which typically carry seeds 0–2 m, and occasionally 30–40 m, from mother plants (Cain *et al.* 1998; Kalisz *et al.* 1999). For wild ginger (*Asarum canadense*), Cain *et al.* (1998) showed that with highly favourable conditions for population growth and with ants as the sole vector of seed dispersal, this species could have migrated *c.* 14 km since the most recent continental glaciers began to recede 21 000 years ago

(Williams *et al.* 2004). This result is at odds with the observation that the geographical distribution of wild ginger presently extends 450 km north of the former southern limit of glacial ice (Cain *et al.* 1998), providing a striking example of Reid's paradox of plant migration (Clark *et al.* 1998). How did ant-dispersed forest herbs, such as *Trillium* and *Asarum*, manage to migrate so rapidly? Having found germinable *T. grandiflorum* seeds in white-tailed deer faeces, Vellend *et al.* (2003) used data on movement patterns and gut-retention times in deer to show that deer may disperse trillium seeds up to 3.8 km, thereby pointing to a potential resolution of this paradox. However, deer influence potential trillium migration not only via the dispersal of seeds, but also via negative effects of herbivory on population demography. Recent studies by Knight (2003, 2004) permit a detailed quantification of the effects of deer on *T. grandiflorum* demography, which we combine here with the deer-generated seed shadow in Vellend *et al.* (2003) to ask how deer herbivory and seed dispersal influence the potential migration rate of *T. grandiflorum*. To put our estimated migration rates in context, we first analyse the present geographical distribution of *T. grandiflorum* in relation to the former extent of continental glaciers. Implications for future migrations are addressed in the discussion, where we conclude that deer herbivory and conditions for population growth may constrain the ability of *T. grandiflorum* to track future climate change.

MATERIALS AND METHODS

Estimating post-glacial migration rates

We estimated the minimum post-glacial migration distance for *T. grandiflorum* by first using ArcMap 9.0 (ESRI, Redlands, CA, USA) to georeference and digitize the range map for *T. grandiflorum* presented by Patrick (1973), in which 965 occurrences (summarized from 2200 herbarium specimens) were located on a map of eastern North America. We then calculated the minimum distance between points along the northern range margin and the former southern extent of glacial ice (taken from Dyke *et al.* 2003). The largest of these values represents the minimum migration distance for *T. grandiflorum* during the late-glacial and Holocene, assuming there were populations near the glacial boundary 21 000 years ago. The present-day distribution of *T. grandiflorum* is most closely associated with the 'cool mixed forest' and 'temperate deciduous forest' biomes as illustrated in the maps of Williams *et al.* (2004). According to vegetation reconstructions based on fossil pollen, cool mixed forest occurred along parts of the southern edge of glacial ice at 21 000 BP, and temperate deciduous forest first appeared in a recognizable form in the southeastern USA (Williams *et al.* 2004). As a reasonable estimate of the

maximum distance *T. grandiflorum* may have migrated in the past 21 000 years, we also calculated the distance from the southeastern USA (near the Gulf of Mexico) to the northern edge of *T. grandiflorum*'s present geographical range.

The model

We used the stage-structured spread model of Neubert & Caswell (2000) to calculate potential migration rates for *T. grandiflorum* at different levels of deer herbivory, and under different assumptions concerning demographic and dispersal processes. This model couples demographic transition matrices for structured populations (as is the case for *T. grandiflorum*) with an integrodifference model of dispersal for different life stages (deer-dispersed seeds in this case) to calculate the asymptotic rate of spread, which we interpret as a migration rate. This model assumes matrix transitions are constant through time and not density dependent. Redistribution of dispersing stages in each time step is described by a probability density function for the distance an individual propagule is dispersed. This function is known as the dispersal kernel. We used the histogram estimator, modified for spread in two dimensions (Lewis *et al.* 2006), to estimate the dispersal kernel from the histogram in Vellend *et al.* (2003). As adults are immobile, we consider dispersal of seeds only. For each of three demographic scenarios (described below), we obtained an estimate of the asymptotic wave speed as follows (Neubert & Caswell 2000): (i) we generated the matrix $\mathbf{H}(s)$, the Hadamard product of the transition matrix and the matrix of moment generating functions for stage-specific dispersal kernels (the delta function is used as the kernel for all non-dispersing stages); the parameter s can be interpreted as governing the steepness of the invasion wave (Lewis *et al.* 2006); (ii) we estimated s^* as the value which minimizes $\alpha(s) = 1/s \log_e \rho_1(s)$, where $\rho_1(s)$ is the dominant eigenvalue of \mathbf{H} ; then (iii) $\alpha(s^*)$ is the asymptotic wave speed.

Species biology

Trillium grandiflorum is a perennial forest herb that may spend 10 or more years in a vegetative state, first as a small one-leaved plant, and subsequently as a three-leaved adult (Patrick 1973). Deer browse almost exclusively on large three-leaved plants, both reproductive and non-reproductive, and deer-browsed plants are more likely to revert to smaller size classes and less likely to become or remain reproductive than non-browsed plants (Knight 2003). As population growth rate (λ) is most sensitive to these transitions, deer herbivory has a strong negative effect on λ (Rooney & Gross 2003; Knight 2004). Because of resource storage in the rhizome of larger plants, a single bout of herbivory (which removes all leaf and reproductive tissue) does not kill plants,

although re-emergence of above-ground tissue will not occur until the following year. Herbivory on reproductive plants may occur early in the growing season when *T. grandiflorum* is in flower (May to June), which eliminates the possibility of seed production, or late in the season (July to August), at which time viable seeds will be ingested, some of which are defecated intact (Vellend *et al.* 2003). Late-season herbivory has no effect on plant size or reproductive state in the following year (Knight 2003), presumably because the vast majority of photosynthesis and translocation of carbohydrate to the rhizome occurs early in the season.

Demography

Knight (2004) recognized six life-history stages for demographic analysis of *T. grandiflorum*: germinant (germinated seed with roots; no leaves are produced in the first year following seed dispersal), seedling (a single cotyledon), one-leaf plants, small three-leaved plants (< 5 cm leaf length), large three-leaved plants (> 5 cm leaf length) and reproductive plants. This species has no dormant seed bank beyond the one winter between dispersal and germination (or death), and reproductive plants consist of a single whorl of leaves with a single flower, which produces a single fruit typically containing five to 30 seeds. Knight (2003, 2004) observed demographic transitions of browsed and non-browsed plants in nine populations over 3 years, and in three other populations over 4 years, for a total of 39 year-to-year transitions and 5796 individual plant transitions. At each population, seed germination rates were calculated from seed baskets established in 2000 and 2001. Each seed basket contained 30 seeds, and was replicated 20 times at each population and year. For each population-year combination, a demographic transition matrix (Caswell 2001) was calculated.

In the present study, we used three demographic scenarios as starting points for our analyses (see Table 1). In all three, deer-browsed plants were first removed from the data before estimating matrix elements. Effects of deer herbivory on different transitions were then added based on their average effects calculated across all populations and years, as described below. The first scenario was the average of the 39 transition matrices ($\lambda = 1.036$). This scenario represents an assumption that past and future conditions for population growth resemble those in the contemporary landscape. In contrast, models of post-glacial migration often assume that conditions for population growth were more favourable in recently glaciated terrain than in present-day populations occupying mature, closed forest (Cain *et al.* 1998; Clark *et al.* 2003). We used two scenarios representing particularly favourable conditions for population growth: the population-year combination showing the greatest potential population growth in the absence of deer ($\lambda =$

Table 1 Demographic transition matrices for *Trillium grandiflorum* populations in the absence of deer herbivory: (a) the average matrix across 39 population-year combinations (population growth rate, $\lambda = 1.036$); (b) the population-year combination with the highest population growth rate ($\lambda = 1.1564$); (c) a composite matrix in which the best value of each transition (in terms of population growth) across populations and years was used, with the constraint that survival rates for a given stage do not exceed 100% ($\lambda = 1.4865$)

Stage at time $t + 1$	Stage at time t						
	1	2	3	4	5	6	7
(a)							
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0	11.36
3	0.314	0.314	0	0	0	0	0
4	0	0	0.311	0.615	0.022	0	0
5	0	0	0	0.134	0.805	0.119	0
6	0	0	0	0	0.113	0.655	0.273
7	0	0	0	0	0	0.226	0.727
(b)							
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0	22.31
3	0.822	0.822	0	0	0	0	0
4	0	0	0.375	0.583	0	0	0
5	0	0	0	0.083	0.81	0.111	0
6	0	0	0	0	0.19	0.593	0.205
7	0	0	0	0	0	0.296	0.795
(c)							
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0	22.31
3	0.822	0.822	0	0	0	0	0
4	0	0	0.667	0.8	0	0	0
5	0	0	0	0.2	0.5	0	0
6	0	0	0	0	0.5	0.222	0.043
7	0	0	0	0	0	0.778	0.957

1, germinant dispersed by deer; 2, germinant not dispersed by deer; 3, seedling; 4, one-leaf plants; 5, small three-leaved plants; 6, large three-leaved plants; 7, reproductive plants.

1.1564; this approach was taken by Cain *et al.* 1998), and a composite transition matrix in which the best value of each transition (in terms of population growth) across populations and years was used, with the constraint that survival rates for a given stage do not exceed 100% ($\lambda = 1.4865$). Although unrealistic for established populations in the present-day landscape, this latter scenario represents a potential upper bound to population growth in small populations establishing in particularly favourable conditions. Although we have no way of studying trillium demography in past environments, introduction of perennial forest herbs into unoccupied post-agricultural forests has shown that newly establishing populations can grow quite rapidly ($\lambda > 1.5$, Petersen & Philipp 2001), suggesting that

the latter scenario is not an unreasonable upper limit to the potential for population growth during migration.

For this paper, we redefined the germinant stage as ‘germinants not dispersed by deer’, and added an additional ‘germinants dispersed by deer’ stage, thereby creating a 7×7 transition matrix, \mathbf{A} (see Table 1). Germinants not dispersed by deer are assumed not to move and (like other sedentary classes) are given the delta function for dispersal kernel. We assumed that the germinant–seedling transition did not depend on whether or not seeds were dispersed by deer; i.e. $\mathbf{A}(2,1) = \mathbf{A}(2,2)$. The three no-herbivory transition matrices were modified to include the effects of herbivory using calculations based on the combined data set across all populations and years as follows. First, reproductive plants browsed early in the season served as a reference point for scaling the proportion of plants browsed in different stages. For each reproductive plant browsed early, 0.222 reproductive plants were browsed late in the season and 0.943 large non-reproductive plants were browsed early. (Late herbivory on non-reproductive plants has no influence on their probability of making different demographic transitions.) The probability of a browsed reproductive plant remaining reproductive is 0.218 that of a non-browsed plant. The corresponding multiplication factor for the large three-leaved plant – reproductive transition was 0.0187, and for the large three-leaved – large three-leaved transition it was 0.501. The probabilities of reproductive and large three-leaved plants regressing by one size class were calculated so that survival of these stages summed to one. To illustrate for one of the transitions, if $\mathbf{A}_{\text{no deer}}$ represents the transition matrix with no deer herbivory, then $\mathbf{A}(7,6)$ at $x\%$ early deer herbivory on reproductive plants is

$$\mathbf{A}_{\text{no deer}}(7,6) - \left(\frac{x}{100}\right) \times 0.943 \\ \times [\mathbf{A}_{\text{no deer}}(7,6) - \mathbf{A}_{\text{no deer}}(7,6) \times 0.0187].$$

Dispersal

All browsed reproductive plants cause a reduction in the production of germinants not dispersed by deer, but reproductive plants browsed late cause an increase in germinants dispersed by deer. However, not all seeds ingested by deer will be defecated intact, and this is the part of the dispersal process on which we have the least information. For a species with seeds of similar size (*Trifolium stoloniferum*, running buffalo clover), Ford *et al.* (2003) found that 27% of seeds fed to white-tailed deer were defecated intact, with similar germination rates as control seeds. Clover seeds tend to be harder than trillium seeds (M. Vellend, personal observation), so a smaller proportion of trillium seeds is likely to survive mastication and digestion by deer. Mouissie *et al.* (2005) measured rates of passage of

germinable seeds of 25 species through fallow deer, which are smaller than whitetails and therefore less likely to pass large seeds. No seeds of the species with the largest seeds (9.5 mg) passed intact, but the range for the other 24 species was 0.5–42% (Mouissie *et al.* 2005). (*Trillium* seed mass is \approx 5 mg; M. Vellend, personal observation.) We explored models assuming proportions of 0.01 or 0.25 for ingested seeds that are defecated intact and with the same germination rate as other seeds; we consider 0.01 a conservative lower limit for this parameter.

All deer-dispersed seeds are assumed to follow the seed shadow reported in Vellend *et al.* (2003). This seed shadow is reasonably well described by a log-normal distribution with a peak at 300–400 m. However, as this distribution fits poorly in the tail and is unsuitable as a dispersal kernel for the Neubert–Caswell model (the moment-generating function is infinite although the log-normal distribution has finite moments), we used the empirical seed shadow with the finite upper limit (3.8 km) given by the maximum of the histogram in Vellend *et al.* (2003). We thus also avoid the problem inherent in models with ‘fat tailed’ dispersal that a non-negligible fraction is dispersed unrealistic distances (Higgins *et al.* 2003). We also assumed that seeds dispersed by ants make no appreciable contribution to migration rate – a reasonable assumption given that *T. grandiflorum* seeds are generally dispersed no further than 10–15 m by ants (Kalisz *et al.* 1999), and that our estimates of migration rates generally exceed by 1–2 orders of magnitude those reported by Cain *et al.* (1998) for wild ginger with seeds dispersed by ants. As it is known that deer may very occasionally move upwards of 10 km over the period during which seeds pass through the gut (Marchinton & Hirth 1984), we explored models in which we allowed 1/10 000 seeds to be dispersed according to a uniform distribution between 3.8 and 10 km.

In sum, we explored the effects of deer herbivory on migration rates under three different demographic scenarios, two different values for the proportion of seeds eaten that are defecated intact (0.01, 0.25), and two different dispersal scenarios (maximum distance 3.8 or 10 km). In addition, as dispersal by deer depends on plants being browsed late in the season, we also explored three scenarios of how the number of late-browsed reproductive plants scales with early browsed reproductive plants (0.222 – the average mentioned above, 0.05 and 0.5).

RESULTS

Trillium grandiflorum migrated no less than 580 km over the last 21 000 years, from the glacial margin in southeastern Massachusetts (beyond which there was land during the Pleistocene) to the area around Trois-Rivières, Québec, at the point in *T. grandiflorum*'s distribution that is furthest north of the southern glacial limit (Fig. 1). If *T. grandiflorum*'s

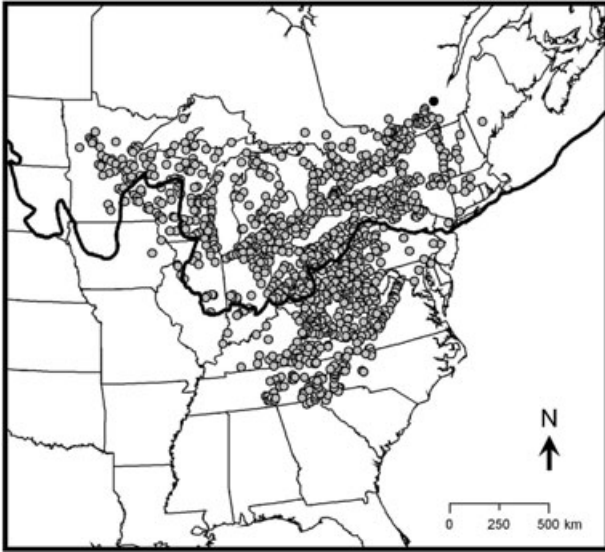


Figure 1 Map of eastern North America showing the southern limit of glacial ice 21 000 years ago (thick solid line; from Dyke *et al.* 2003), and the current distribution of *Trillium grandiflorum* (grey circles; from Patrick 1973). The filled black circle shows the point in *T. grandiflorum*'s distribution that is furthest north of the glacial boundary, 580 km, which represents the minimum migration distance during the past 21 000 years.

Pleistocene refugium was in the southeastern USA, it may have migrated as far as 2000 km over the past 21 000 years. For comparison with these two benchmark distances, in all cases we rescaled predicted migration rates to illustrate the distance covered during 21 000 years.

Under each of the three demographic scenarios we used results for proportion of seeds passed intact = 0.01, maximum dispersal = 3.8 km, and the scaling of late : early herbivory on reproductives = 0.222 as the basis of comparison because this represents a conservative scenario with respect to predicting high migration rates. Note that in Fig. 2 herbivory is plotted as the proportion of reproductive plants browsed, both early and late.

Under all scenarios, migration rate was greatest at an intermediate level of deer herbivory, although this level was always < 15%. Without seed dispersal by deer, the potential migration rate is negligible (an assumption of the model), but even with very low levels of deer herbivory (< 1%) migration distances on the order of hundreds or thousands of km during 21 000 years are predicted. Beyond 10–15% herbivory, potential migration rate declines strongly.

The three demographic scenarios predict migration rates that vary over an order of magnitude. Using the average of observed transition matrices, the maximum predicted migration distance was < 300 km, regardless of other model assumptions, and above *c.* 20% herbivory, migration is not possible at all because $\lambda < 1$. In the two favourable

demographic scenarios, $\lambda > 1$ even at 100% herbivory on reproductive plants because some seeds survive passage through the deer gut, and rates of successful germination, establishment and growth of small plants are sufficiently high (Table 1) to maintain viable populations.

Relative to the effect of demography, the proportion of seeds that survive passage through a deer gut had relatively little influence on predicted migration rates. A 25-fold increase in this proportion (0.01–0.25) resulted in only a 20–25% increase in maximum migration rate (Fig. 2a–c). In contrast, allowing a very small fraction (1/10 000) of seeds to disperse as far as 10 km almost doubled potential migration rates, and in the most favourable demographic scenario the maximum predicted migration distance was > 3000 km (Fig. 2d–f). Varying the proportions of reproductive plants browsed early vs. late had effects on potential migration rates similarly small in magnitude to the effect of proportional seed passage (Fig. 2g–i).

DISCUSSION

Our analysis revealed a clear antagonism between the effects of seed dispersal and herbivory by deer on the potential migration rate of *T. grandiflorum*, and we suspect that the qualitative nature of this antagonism applies broadly to the many plant species whose seeds are dispersed by herbivores or seed predators. For *T. grandiflorum*, dispersal by deer permits migration rates that fit patterns of northern range expansion during rapid climate change, but the negative effects of deer on population growth may severely compromise the potential for tracking suitable climatic conditions during migration. If population growth in the absence of deer is relatively slow (the 'average' scenario), migration is not possible at all at > 20% deer herbivory because *T. grandiflorum* populations are doomed to extinction (Fig. 2a,d,g). In the Pennsylvania *T. grandiflorum* populations studied by Knight (2003, 2004), the average level of deer herbivory on reproductive plants was 18%, ranging from 0% to 60% in different populations and years. In Wisconsin, Rooney & Gross (2003) found 0–30% herbivory across nine sites (mean = 8–9% across 2 years). Thus, current average levels of deer herbivory exceed that which is optimal for migration given the 'average' demographic scenario, but are quite close to that which is optimal under favourable demographic scenarios. Given that the density of white-tailed deer in parts of eastern North America (including Pennsylvania and Wisconsin) is currently upwards of 10–50 km⁻² compared with an estimated 3–4 km⁻² prior to European settlement (McShea *et al.* 1997), deer at relatively low densities quite likely made a major contribution to the post-glacial migration of *T. grandiflorum*.

It is impossible to know accurately how conditions during the late glacial and Holocene affected different aspects of

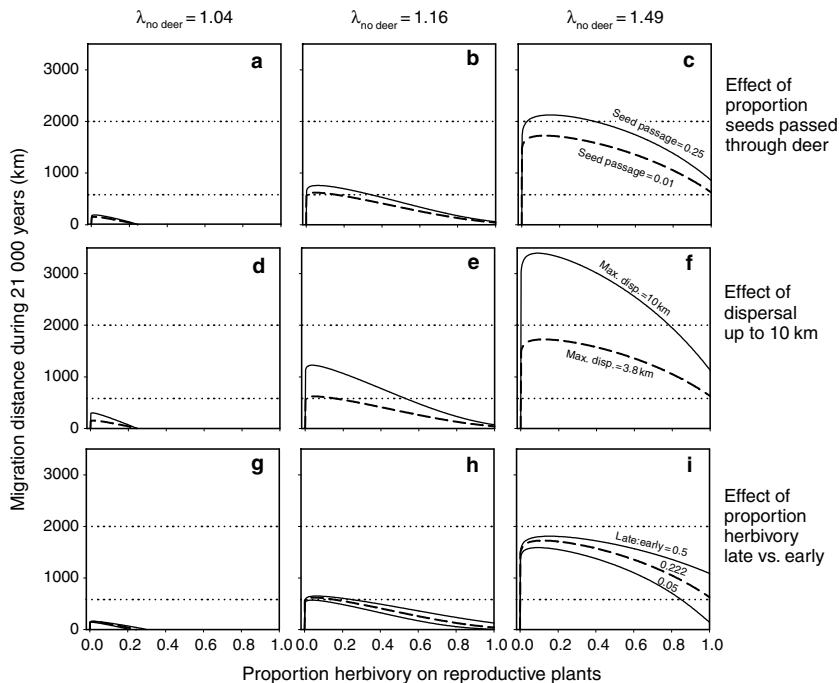


Figure 2 The effect of per cent deer herbivory on the potential migration distance of *Trillium grandiflorum* during the past 21 000 years under three demographic scenarios varying from low population growth rates in the absence of deer ($\lambda_{\text{no deer}}$) on the left to high $\lambda_{\text{no deer}}$ on the right (see Table 1). Horizontal dotted lines indicate the minimum (580 km) and maximum (2000 km) possible distances covered by *T. grandiflorum* during post-glacial migration. In all panels the dashed line shows results for proportion of seeds passed intact = 0.01, maximum dispersal = 3.8 km, and the scaling of late : early herbivory on reproductive = 0.222. (a–c) Solid lines show results for proportion of seeds passed intact = 0.25; (d–f) solid lines show results for 1/10 000 seeds dispersed up to 10 km; (g–i) solid lines show results for late : early herbivory = 0.05 (lower lines) or 0.5 (upper lines).

plant migration, although some inferences based on historical data are possible. Fortunately, the one aspect of the dispersal process about which we had the least information (proportional passage through a deer's gut) had relatively little impact on potential migration rate (Fig. 2a–c). With respect to the starting point of post-glacial migration, the most likely scenario was that *T. grandiflorum* had at least some small populations within a few 100 km of the glacial margin. Recent re-evaluations of fossil pollen data and phylogeographical analyses suggest that tree taxa closely associated with *T. grandiflorum* (*Acer* and *Fagus*), had populations right at the glacial margin at the onset of the Holocene (McLachlan *et al.* 2005). A phylogeographical analysis of *T. grandiflorum* by Griffin & Barrett (2004) had relatively low power to distinguish competing historical hypotheses, but the resulting patterns were consistent with those in *Acer* and *Fagus*. All five observed chloroplast-DNA haplotypes were found both south and north of the glacial margin, and there was no clear evidence of glacial refugia occurring towards the southern end of *T. grandiflorum*'s range (Griffin & Barrett 2004). Thus, *T. grandiflorum* most likely migrated 580–800 km over the last 21 000 years, although of course the rate of migration may well have exceeded 800 km per 21 000 years given that the northern range limit may have been reached long before the present day. With respect to seed dispersal, it seems most realistic to assume that some very small fraction seeds would be dispersed upwards of 10 km each year during post-glacial migration (see Materials and methods), particularly given that deer were also migrating northward at that time (white-tailed deer

currently occur > 1000 km north of the glacial margin). There may, of course, have been other agents of long-distance dispersal of which we are unaware, such as the now-extinct passenger pigeon (*Ectopistes migratorius*, e.g. Webb 1986), but to date white-tailed deer represent the only documented seed dispersal vector that can move *Trillium* seeds > 1 km.

Assuming deer herbivory < 20% and seed dispersal up to 10 km, we can easily explain migration distances > 580 km during 21 000 years if we additionally assume that environmental conditions were quite favourable for population growth (Fig. 2). This latter assumption is most difficult to evaluate. Past analyses of post-glacial migration have typically assumed relatively high values of λ , and framed Reid's paradox as an issue of how seeds could have been dispersed as far as is needed to explain rapid migration (Cain *et al.* 1998; Clark *et al.* 1998). Our results flip this issue on its head by suggesting that, at least in this case, an equally valid question is why were conditions for population demography apparently so favourable during post-glacial migration? Recently deglaciated terrain may be rapidly colonized by plants, as in Glacier Bay, Alaska (Chapin *et al.* 1994), but only a subset of plant species find such conditions particularly favourable for population growth. Most of the populations studied by Knight (2003, 2004) were at quite low densities, so it is unlikely that the low density of establishing populations during post-glacial migration provides an explanation for why population growth rates may have been particularly high during post-glacial migration. For the moment, we must assume that perennial forest

herbs with distributions many hundreds of km north of former glacial ice experienced very favourable conditions for population growth in recently deglaciated terrain during the Holocene. It remains an open question as to how many species have present distributions that remain out of equilibrium with climatic conditions given slow potential migration rates.

For plant species in the north-temperate zone to track projected climate change over the next 100–200 years, migration rates at least as fast as those achieved during post-glacial migration will be required (Malcolm *et al.* 2002). Under the assumption of a doubling of atmospheric CO₂ concentrations over the next century and using several different combinations of global circulation and vegetation models, Malcolm *et al.* (2002) estimated required migration rates on the order of 0.1–1 km year⁻¹ for temperate mixed forests, which corresponds to approximately 2000–20 000 km over a period of 21 000 years. Our estimates of potential migration rates exceed the lower end of this range under some scenarios (see Fig. 2), but post-glacial migration rates may overestimate the potential rate of future migration in response to anthropogenic climate change for several reasons. First, unlike during post-glacial migrations, present-day landscapes in eastern North America are not undergoing primary succession, which may have favoured rapid population growth in the past. The ‘average’ scenario of population growth, under which migration was relatively slow, may represent the most realistic assumption for forecasting the response of *T. grandiflorum* to future climate change. Under this demographic scenario, present levels of deer herbivory of *c.* 10% further constrain the potential migration rate. Finally, habitat fragmentation may result in a relatively high proportion of deer-dispersed seeds landing in unsuitable habitats (e.g. agricultural fields), although this is essentially equivalent to seed loss during mastication or digestion, which had relatively little effect on migration potential (Fig. 2a–c). In sum, although we are sufficiently ignorant of how future conditions will influence plant demography and dispersal to make accurate forecasts, there appears to be good reason to suspect that many plant species will be unable to track anthropogenically driven changes in climate.

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REFERENCES

- Baker, R.R. (1978). *The Evolutionary Ecology of Animal Migration*. Holmes and Meier Publishers, Inc., New York, NY.
- Cain, M.L., Damman, H. & Muir, A. (1998). Seed dispersal and the Holocene migration of woodland herbs. *Ecol. Monogr.*, 68, 325–347.
- Caswell, H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd edn. Sinauer, Sunderland, MA, USA.
- Chapin, F.S. III, Walker, L.R., Fastie, C.L. & Sharman, L.C. (1994). Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol. Monogr.*, 64, 149–175.
- Clark, J.S., Fastie, C.F., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A. *et al.* (1998). Reid’s paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. *Bioscience*, 48, 13–24.
- Clark, J.S., Lewis, M., McLachlan, J.S. & HilleRisLambers, J. (2003). Estimating population spread: what can we forecast and how well? *Ecology*, 84, 1979–1988.
- Dyke, A.S., Moore, A. & Robertson, L. (2003). *Deglaciation of North America*. Open File Report 1574. Geological Survey of Canada, Calgary, AB.
- Ford, W.M., Madarish, D., Schuler, T.M. & Castleberry, S.B. (2003). Influence of white-tailed deer digestion on running buffalo clover (*Trifolium stoloniferum*: Fabaceae Muhl. ex A. Eaton) germination. *Am. Midl. Nat.*, 149, 425–428.
- Griffin, S.R. & Barrett, S.C.H. (2004). Post-glacial history of *Trillium grandiflorum* (Melanthiaceae) in eastern North America: inferences from phylogeography. *Am. J. Bot.*, 91, 465–473.
- Higgins, S.I., Clark, J.S., Nathan, R., Hovestadt, T., Schurr, F., Fragoso, J.M.V. *et al.* (2003). Forecasting plant migration rates: managing uncertainty for risk assessment. *J. Ecol.*, 91, 341–347.
- Jackson, S.T. & Overpeck, J.T. (2000). Responses of plant populations and communities to environmental changes of the late quaternary. *Paleobiology*, 26 (Suppl.), 194–220.
- Kalisz, S., Hanzawa, F.M., Tonsor, S.J., Thiede, D.A. & Voigt, S. (1999). Ant-mediated seed dispersal alters spatial pattern of seed relatedness in an outcrossing population of *Trillium grandiflorum*. *Ecology*, 80, 2620–2634.
- Knight, T.M. (2003). Effects of herbivory and its timing across populations of *Trillium grandiflorum* (Liliaceae). *Am. J. Bot.*, 90, 1207–1214.
- Knight, T.M. (2004). The effects of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. *Ecol. Appl.*, 14, 915–928.
- Lewis, M., Neubert, M.G., Caswell, H., Clark, J.S. & Shea, K. (2006). A guide to calculating discrete-time invasion rates from data. In: *Conceptual Ecology and Invasions Biology: Reciprocal Approaches to Nature* (eds Cadotte, M.W., McMahon, S.M. & Fukami, T.). Kluwer, Dordrecht, The Netherlands (in press).
- Malcolm, J.R., Markham, A., Neilson, R.P. & Garaci, M. (2002). Estimated migration rates under scenarios of global climate change. *J. Biogeogr.*, 29, 835–849.
- Marchinton, R.L. & Hirth, D.H. (1984). Behavior. In: *White-Tailed Deer: Ecology and Management* (ed. Halls, L.K.). Stackpole Books, Harrisburg, PA, USA, pp. 129–168.
- McLachlan, J.S., Clark, J.S. & Manos, P.S. (2005). Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, 86, 2088–2098.

- McShea, J.W., Underwood, H.B. & Rappole, J.H. (eds) (1997). *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington, DC.
- Mouissie, A.M., van der Veen, C.E.J., Veen, G.F. & van Diggelen, R. (2005). Ecological correlates of seed survival after ingestion by fallow deer. *Funct. Ecol.*, 19, 284–290.
- Myers, J.A., Vellend, M., Gardescu, S. & Marks, P.L. (2004). Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia*, 139, 35–44.
- Neubert, M.G. & Caswell, H. (2000). Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, 81, 1613–1628.
- Patrick, T.S. (1973). Observations on the life history of *Trillium grandiflorum* (Michaux) Salisbury. MSc Thesis, Cornell University, Ithaca, NY, USA.
- Petersen, P.M. & Philipp, M. (2001). Implantation of forest plants in a wood on former arable land: a ten year experiment. *Flora*, 196, 286–291.
- van der Pijl, L. (1982). *Principles of Dispersal in Higher Plants*. Springer-Verlag, New York, NY.
- Rooney, T.P. & Gross, K. (2003). A demographic study of deer browsing impacts on *Trillium grandiflorum*. *Plant Ecol.*, 168, 267–277.
- Vellend, M., Myers, J.A., Gardescu, S. & Marks, P.L. (2003). Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology*, 84, 1067–1072.
- Webb, S.L. (1986). Potential role of passenger pigeons and other vertebrates in the rapid Holocene migrations of nut trees. *Q. Rev.*, 26, 367–375.
- Williams, J.W., Shuman, B.N., Webb, T. III, Bartlein, P.J. & Leduc, P.L. (2004). Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecol. Monogr.*, 74, 309–334.

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