



Factors influencing tree colonization in fragmented forests: an experimental study of introduced seeds and seedlings

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Abstract

Plant colonization is essential to maintain diversity in fragmented ecosystems, but there is little experimental information on this process. We used experimental seed and seedling transplantation to evaluate the ability of the seed of tree species to become established in Southern Ontario forest fragments not containing the species. *Carya cordiformis* (Wang.) K. Koch, *Betula alleghaniensis* Britton, *Fagus grandifolia* Ehrh. and *Juglans nigra* L. were introduced into the interiors of (1) woodlots not containing members of their species (uncolonized woodlots), (2) woodlots containing conspecifics (colonized woodlots), and (3) well-illuminated sites at the edges of the uncolonized woodlots. With these data, we evaluated the probabilities of seedling colonization by the species and tested the predictions that survival rates are higher in uncolonized woodlots due to escape from host-specific predators and pathogens (Escape hypothesis), and colonization is promoted by seed arrival in well-illuminated sites at forest edges (Edge hypothesis). Both predictions were supported for a subset of the species, indicating two factors that may facilitate colonization. However, the influence of these factors occurred mainly after the second year of seedling establishment and overall survivorship was low due to high rates of mortality among seeds, germinating and first year seedlings. Probabilities of fourth year seedling establishment in uncolonized woodlots were <1% of incoming seed for three of the four species. Successful colonization of these species will depend on relatively large seed inputs to fragments. A previous study indicated that dispersal to and establishment in fragments >150–175 m from a seed source occurs at a rate of less than 1 seedling/ha over a 4–11-year period. Therefore, management intervention such as seedling transplantation may be necessary to maintain eastern deciduous tree species in fragmented forests.

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1. Introduction

Over the last 200 years, the forests of central and eastern North America have been transformed from extensive and relatively continuous communities into

patchworks of isolated remnants (Curtis, 1956; Burgess and Sharpe, 1981). While reforestation has occurred in places such as New England (Foster, 1992), large areas of fragmented forest remain. This change in the biogeography of forest ecosystems may be expected to produce species extinctions (MacArthur and Wilson, 1967; Diamond, 1975; Tramer and Suhrweir, 1975). Local, within-fragment, extinctions may be accelerated by reduced habitat and population sizes

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and environmental changes resulting from increased forest edge-to-interior ratios (Shaffer, 1981; Lovejoy et al., 1986; Kapos, 1989; Williams-Linera, 1990; Matlack, 1993). Inter-fragment migration, necessary to offset local extinctions and maintain diversity, is likely to be constrained by the long distances and potentially “hostile” matrices separating fragments (DeAngelis et al., 1979; Goodman, 1987; Burkey, 1989). However, there is a lack of quantitative information on tree migration processes in fragmented landscapes with which to test these predictions. In a previous study, we examined the abilities of 29 hardwood tree species to disperse long distances between forest patches in a fragmented eastern deciduous forest system (Hewitt and Kellman, 2002a,b). The present study investigates post-dispersal seedling establishment in forest fragments not already containing the species. In particular, we investigate two conditions that may promote seedling colonization in fragments, spatial isolation from conspecifics hosting natural enemies (Escape hypothesis), and the presence of well-illuminated sites, in this case, found at forest edges (Edge hypothesis). By focusing on seeds and seedlings, much of the demographic uncertainty in tree colonization could be accounted for since mortality tends to be concentrated in the early life history stages of trees in all-aged forests (Harper, 1977; Silvertown, 1987; Harcombe, 1987).

Several studies have investigated seedling establishment and survivorship in forest fragments (Santos and Tellería, 1997; Benitez-Malvido, 1998; Bruna, 1999, 2002; Restrepo and Vargas, 1999; Scariot, 2001). However, these do not deal with colonization scenarios, and come largely from tropical locales. Thus, the controls on establishment of colonizing species seedlings in temperate forest fragments remain speculative. It might seem unlikely that a colonizing species could easily become established, given that its seed would arrive in very low numbers from distant fragments and be vastly out-numbered by seed of locally producing species. Combined with the high rates of mortality among seeds and seedlings (Harper, 1977), this represents a huge numeric disadvantage. Yet colonizations have occurred repeatedly in the past (e.g., species migrations during climate change, exotic species invasions), suggesting that there are differential benefits to becoming established in new locations, or that special circumstances may periodically facilitate such establishment. The

“Escape” hypothesis (*sensu* Howe and Smallwood, 1982) predicts that seed and seedling mortality will decrease with increasing distance away from parent plants that harbor natural enemies. The natural enemies involved would be those that are specialized with respect to prey and restricted in mobility, such as invertebrate seed and foliage predators and soil-borne fungal pathogens, rather than wide-ranging, generalist mammal predators that may produce density-dependent, but not strongly distance-dependent effects (Janzen, 1970; Connell, 1971; Harper, 1977; Crawley, 1992; Thrall and Burdon, 1997). This hypothesis was originally proposed as a mechanism regulating common species abundances in tropical forests (Janzen, 1970; Connell, 1971) and it has received considerable support (Augspurger, 1983; Clark and Clark, 1984; Howe and Schupp, 1985; Schupp, 1988; but see Condit et al., 1992). These studies primarily involve continuous forest and investigate effects over relatively short distances, typically <50 m. In fragmented landscapes, where long distances and distinct land cover separates populations, the “escape” mechanism might operate more effectively than in continuous communities.

Well-illuminated sites resulting from human or natural disturbance have been implicated in exotic plant species invasions (Elton, 1958; Mack, 1986; Crawley, 1987; Robinson and Edgemon, 1988; Hobbs, 1989; Rejmanek, 1989; Burke and Grime, 1996; Lozon and MacIsaac, 1997), post-glacial tree migrations in North America (Davis, 1987), and may similarly promote migration among fragments. Such sites may be particularly important in productive, light-limited communities such as mesic temperate deciduous forests. Moreover, high light intensity may promote seedling survival through fungal pathogen suppression (Vaartaja, 1952; Augspurger, 1983). In fragmented forests, sites of high illumination would include canopy gaps, either created naturally or artificially, from selective logging activities. The paucity of such sites in some temperate fragmented systems has been attributed to a decline in the numbers of opportunistic tree species (Weaver and Kellman, 1981). In addition to canopy gaps, unique microenvironments at anthropogenic edges may provide additional opportunities for seedling establishment compared to the forest interior. Much has been speculated about the deleterious consequences of edges to plant survival. Conditions such as low humidity and high windspeeds

at edges are common at and near forest edges (Kapos, 1989; Williams-Linera, 1990; Murcia, 1995) and may have negative impacts on survivorship, particularly of shade-tolerant species, compared to conditions within woodlot interior (Ranney et al., 1981; Palik and Murphy, 1990; Williams-Linera, 1990; Saunders et al., 1991). For example, Benitez-Malvido (1998) documented lower seedling densities in small (<1 ha) relative to large (>10 ha) tropical forest fragments, likely due to the intrusion of desiccating conditions from the surrounding landscape. However, the data on tree species responses to edges is scant and often not conclusive (Murcia, 1995). Negative effects may not pertain to all species, or may cease to prevail in older forest edges, once plant distributions and architecture have adjusted to changes and edge tolerant species begin to predominate. The greater light availability at edges may promote establishment and survival of some species in the same way that conditions in a large canopy gap might. While edges may differ from canopy gaps in their potentially greater canopy openness and wind-exposure, field observations suggested that the species composition and plant densities of the two habitats were quite similar in the study area, suggesting that the environments of edges and gaps in this system may be comparable in some ways. Thus, increased light availability occurring both in canopy gaps and a forest edges may facilitate colonization relative to sites in the shady forest interior. Due to a lack of canopy gaps in the study system we used fragment edges to investigate the role of sites of increased light availability on seedling colonization.

2. Materials and methods

2.1. Study area

The study was conducted in a 17 km² area on the north shore of Lake Erie, Southern Ontario (42°40'N, 80°29'W) and lies within the eastern deciduous forest region of North America (Fig. 1a). The climate is humid, temperate (1961–1980 mean annual temperature: 7.9 °C; mean annual rainfall: 847.3 mm) and is moderated by the presence of nearby lake Erie, with cool winters (January mean monthly minimum, maximum temperatures: –9.6, –1.9 °C) and hot, humid summers (July mean monthly minimum, maximum

temperatures: 14.6, 26.5 °C) (Atmospheric Environment Service, 1981). The topography is relatively flat, but interrupted in places by sand dunes created in the immediate post-glacial period. Soils are classified as Brunisolic Gray Brown Luvisols. In the north part of the study area soils tend to be sandy, well drained and slightly acidic. South of the 4th concession road (Fig. 1b), finer-grained glaciolacustrine material becomes exposed and soils are less acidic with greater moisture holding capacity and higher organic matter content (Presant and Acton, 1984; Barnett, 1992). The pre-settlement forest of the region was cleared extensively for agriculture in the 1800s and the remaining woodlots exist in a landscape devoted to the cultivation of cash-crops such as tobacco, corn, and soybeans. Woodlots range in size from under one hectare to 49.0 ha (mean 9.1 ha; $n = 22$) and appear to be cutover remnants of former forest rather than second growth, judging from the size of canopy trees and presence of large stumps. The woodlots are relatively species rich, with larger tracts supporting over 30 native hardwood species and, collectively, containing more than 40 tree species (Hewitt, 1999). Major tree species include *Acer saccharum* Marsh., *A. rubrum* L., *Fagus grandifolia* Ehrh., *Betula alleghaniensis* Britton, *Prunus serotina* Ehrh., *Carya* spp., *Quercus alba* L., and *Quercus rubra* L.. Populations of all tree species are found in the ca. 500 ha forest preserve, Backus Woods (Fig. 1b). Rodent predation from *Sciurus carolinensis*, *S. nigra*, *Tamiascirus* spp. is a major source of post-dispersal seed mortality among nut tree species in eastern forests (pers. obs.; Thompson and Thompson, 1980; Sork, 1984; Price and Jenkins, 1987; Crawley, 1992). Invertebrate larvae are other known seed predators of North American hardwood tree species (Rose and Lindquist, 1982; USDA Forest Service, 1985), though they have not been observed in action by the researchers. Deer (*Odocoileus virginianus*) and mice are important foliage predators in eastern forests, as are various species of invertebrates and pathogens.

2.2. Field methods

To investigate the probabilities of post-dispersal tree colonization, seeds and seedlings of four tree species were introduced into (1) the interiors of woodlots containing conspecifics, as controls (Home sites), (2) the interiors of woodlots not containing

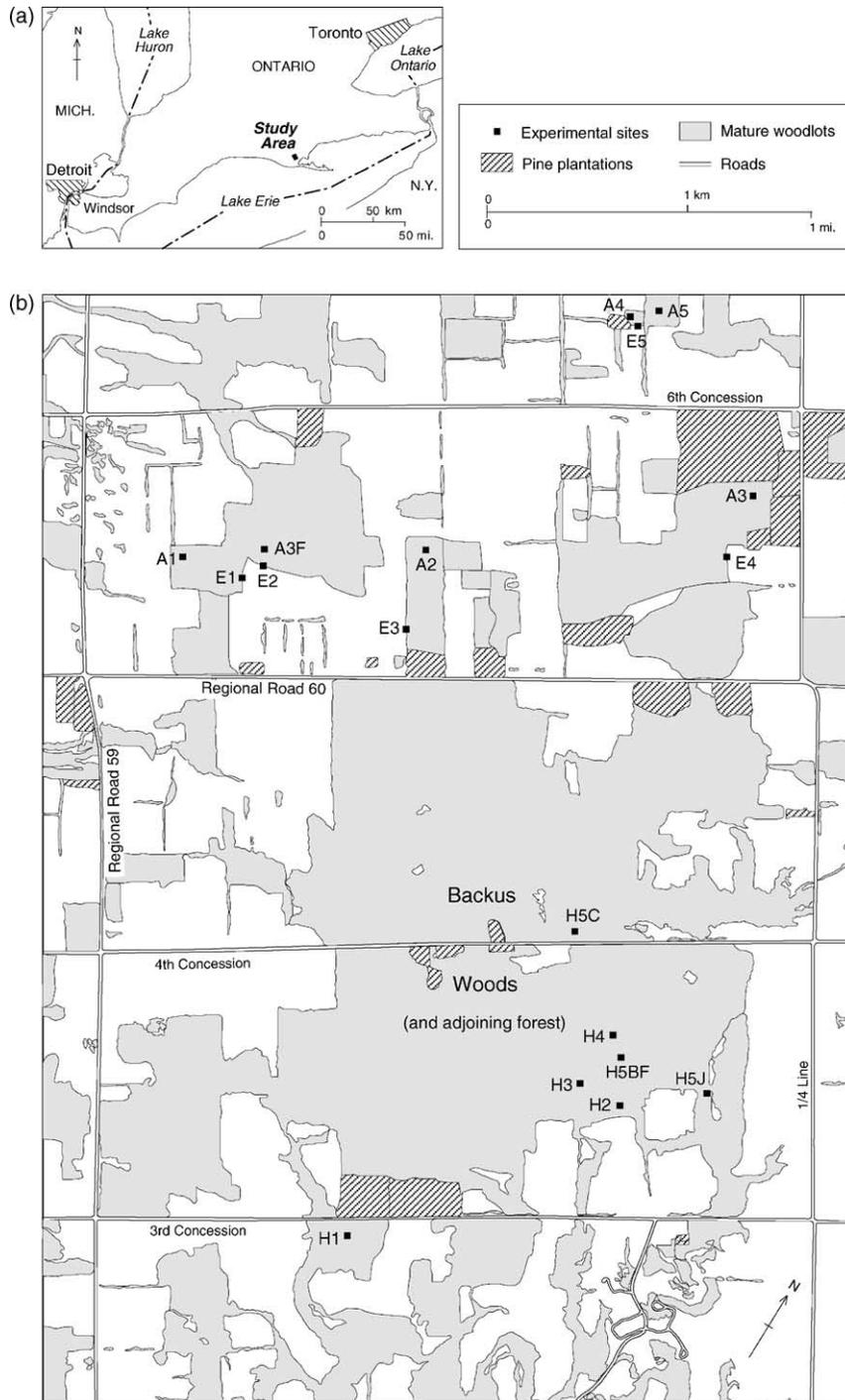


Fig. 1. (a) The location of the study area within Southern Ontario; (b) map of Backus Woods and surrounding study area. Experimental sites are numbered by treatment (Home sites: H1–H5; Away: A1–A5; Edge: E1–E5). Separate species plots include the genus initial (A3F: Away site # 3 for *F. grandifolia*) (after Hewitt and Kellman, 2002a).

Table 1
Characteristics of the four study species^a

Species	Seed mass (g)	Dispersal mechanism	Shade tolerance
<i>B. alleghaniensis</i>	0.001	Wind	Intermediate
<i>C. cordiformis</i>	2.91	Rodent	Shade tolerant
<i>F. grandifolia</i>	0.28	Bird	Very shade tolerant
<i>J. nigra</i>	11.34	Rodent	Shade tolerant

^a Source: USDA Forest Service (1948) and Burns and Honkala (1990).

conspecifics (Away sites), and (3) well-illuminated sites at the edges of Away woodlots (Edge sites). Survival was compared between the Home and Away sites to test the Escape hypothesis that survival will be higher in uncolonized woodlots due to escape from predators and pathogens, and between Away and Edge sites to test the Edge hypothesis that sites of greater light availability may promote survival relative to conditions in forest interiors.

Following woodlot surveys for species composition in May–July 1995, *F. grandifolia*, *C. cordiformis* (Wang.) K. Koch, *J. nigra* L., and *B. alleghaniensis* were selected for study because they were absent or rare in four woodlots in the study area and represented a range of seed sizes, shade-tolerance, and dispersal mechanisms (Table 1). Five replicate Home treatment sites were located in the large tract of forest in and around Backus Woods where the study species were locally abundant and occurred as several discrete populations. Plots were positioned on areas of level ground beneath closed canopy in areas classified as mesic (Varga, 1985). Adult conspecifics were often rooted within the plots or within a distance of 25 m. Five replicate Away plots were established on level ground in four woodlots, with one woodlot containing two replicates separated by >90 m (Fig. 1b). Away and Home sites were located at least 50 m from an edge except for A4 whose north margin was 25 m from an edge. *F. grandifolia* was present though infrequent (one to four stems) in all Away woodlots, but since this species occurred at high densities in Home sites, it was expected to have reduced exposure to specialist predators in Away sites. Away sites were located at least 50 m from *F. grandifolia* stems. Two east-facing, two south-facing and one west-facing Edge sites were located at the margins of woodlots not containing members of the species on areas of relatively undis-

turbed, level ground (Fig. 1b). To reduce competition with herbaceous and shrubby vegetation, we removed aboveground stems of competing species at Edges every 2–3 weeks for the first 2 years of the experiment. After that time, clipping was stopped and competing species were allowed to grow up around transplants. We attempted to find treatment sites that met experimental criteria for all four species to permit a randomized experimental design and statistical comparisons among species as well as treatments. Only one replicate Home site per species and one Away site for *F. grandifolia* contained separate species (Fig. 1b). To ensure adequate sample sizes, separate experiments were used for (a) seed survivorship, (b) germination to first year survival, and (c) second to fourth year survival.

2.3. Seed survivorship experiment

Rodent predation was assumed to be the main cause of seed non-survivorship (see Section 2.1). To assess the importance of rodent seed predation to seed survival and to determine how rates varied among Home and Away sites for these species, ten seeds of *J. nigra*, *F. grandifolia*, and *C. cordiformis* were sown in each of the five Home and five Away sites (50 seeds per species per treatment) during fall, 1996. There was no prediction for seed predation under the Edge hypothesis so predation at Edges was not investigated. *B. alleghaniensis* seeds are not important rodent prey and were not included in the experiment (Burns and Honkala, 1990). Seeds were sown beneath 0.5–1 cm of soil to simulate dispersal by their main dispersers, rodents and bluejays (Cahalane, 1942; Johnson and Adkisson, 1985; Burns and Honkala, 1990) in a grid of alternating species, with 6 m between seeds of different species, minimum or 7.1 m between conspecifics. In sites with single species, seeds were sown 8 m apart. Plots were surveyed in early May 1997 when recovery of winter caches by squirrels has ended (Thompson and Thompson, 1980). Missing seeds were treated as predation events, though some may have survived and been buried elsewhere.

2.4. Seed sowing experiment for germination and first year survival

Twenty seeds per species were sown in each Home, Away, and Edge site (100 seeds per treatment) during

fall 1996 to indicate germination and first year survivorship. Effects of invertebrate seed predation would be encompassed in measures of germination. Seeds of *F. grandifolia*, *C. cordiformis*, and *J. nigra* were sown beneath 0.5–1 cm of soil in single-species rows with 15 cm between seeds and rows at mixed-species sites, 20 cm at single-species sites. Wire mesh (1.3 cm diameter) was fastened over plots to prevent rodent seed predation. Leaf litter was cleared from the plot prior to planting, then redistributed after laying mesh down. Because leaf litter on the forest floor inhibits establishment of *B. alleghaniensis* (Keever, 1973; Burns and Honkala, 1990), seeds of this species were sown on rotting logs by rubbing seeds into the log surface at 20 points, 15 cm apart. Due to the low seed viability of *B. alleghaniensis* compared to the other species (25% compared to >85% for the others), six seeds per point were sown, for a total of 600 seeds per treatment or approximately 150 viable seeds. Seed viability was determined in the lab using the tetrazolium chloride method (Isely, 1952) for the nut tree species and using growth chamber experiments for *B. alleghaniensis*.

Germination and first year survival were recorded every 2–3 weeks from May to July 1997, every 3–4 weeks from July to August 1997, then once in June and in August 1998 to capture delayed germination and seedling survival of *C. cordiformis* and *J. nigra*. The visible condition of seedlings and the presence of adverse agents (e.g., herbivory, desiccation, pathogens) were noted and death attributed to adverse agents present on preceding survey date(s) using the following symptoms: (1) pathogen attack: softening and wilting of the stem, blackening of leaf tips and stem, spots and fruiting bodies, (2) insect herbivory: removal of cotyledons or leaf tissue, (3) mammal herbivory: clipping and removal of the stem with leaves, or evidence of uprooting and removal of the entire plant, (4) desiccation: brittle stems or leaves or reddish-brown patches on leaves, (5) physical damage: stem breakage or burial by woody or leaf litter, (6) unknown: seedling died or disappeared without prior evidence of adverse agents. Death was attributed to insects only if >30% of the cotyledons or >50% of the leaf tissue had been removed. Pathogens were described and classified based on visible features and leaf tissue samples were shipped with field descriptions to the Canadian Forest Research

Institute for taxa identification. Insect species found on plants were described and photographed, and Rose and Lindquist (1982) and USDA Forest Service (1985) used for species identification.

2.5. Seedling transplant experiment for second to fourth year seedling survival

Dormant second-year seedlings of *F. grandifolia*, *C. cordiformis*, and *J. nigra* were obtained from a supplier of locally derived stock and transplanted into the field in late April 1997 (30 per plot; 150 per treatment). *B. alleghaniensis* seedlings were cultivated by the researchers in a growth chamber using seeds obtained from the local supplier. Seeds were refrigerated in moist soil for 4.5 months and spreading them over sterilized potting soil in a growth chamber programmed for a 9 h daylight period and a temperature alternation of 19 °C during darkness and 29 °C during daylight. The 2–3-month-old *B. alleghaniensis* seedlings were transplanted in late May 1997 and again in early June to replace May transplants that had died, and were watered in the first week following transplantation. At Home and Away sites, seedlings were transplanted in rows of alternating species with 1 m between seedlings of different species, minimum of 3.3 m between conspecifics, maximum of 4 m. In the single species sites, seedlings were 2 m apart. At Edge sites, seedlings were planted in 20 rows, perpendicular to the edge and beginning just beneath the limit of overhanging tree canopy, and were 1 m apart. There were 3 m between conspecifics within rows, 1.9–2 m between rows, and 0.75 m between seedlings of different species in rows.

To prevent predation by mammals, assumed not to be important in differentiating Home and Away sites under the Escape hypothesis, seedling stems and branches were painted with “Scoot”, a bitter-tasting mammal repellent, upon transplantation and at the beginning and end of the first two growing seasons. The repellent does not affect invertebrates or pathogens. A separate, smaller experiment involving unprotected seedlings was used to indicate rates of mammal herbivory for the species generally. In this, 10 seedlings per species were transplanted in Home and Away sites (50 seedlings per species per treatment) in plots 20 m away from the main seedling transplant plots. Between-seedling distances were doubled in this experiment since wide ranging mammals might otherwise destroy

all seedlings within plots. *B. alleghaniensis* was not included as insufficient numbers of seedlings remained from main plots.

Seedling survivorship was monitored every 3–4 weeks from May to September 1996, May to August 1997, and again in June and August 1998. Adverse agents were recorded in 1996 and 1997 to explain cause of death. Seedling growth and leaf number were used as performance measures. Seedling height, from base of the plant to the tallest apical meristem in *J. nigra* and *C. cordiformis*, and to the top of the tallest branch pulled straight for *F. grandifolia* and *B. alleghaniensis*, was measured in May 1996 and on the last survey date in 1996 and 1997 and change in height used to indicate growth rate. Plants that had lost stem tissue to herbivory or wilting were excluded. Leaf number was measured in August 1997. Each compound leaf for *J. nigra* and *C. cordiformis* was counted as a single leaf.

2.6. Environmental conditions

To evaluate the comparability of experimental plot environments, we measured light levels, percent soil moisture, leaf litter depth, and tree species composition at all treatment sites. The ozalid paper technique (Friend, 1961; Sullivan and Mix, 1982) was used to measure daily cumulative light input at ground level during 1 day in late July 1996 and 1997 at 10 randomly located points in Home and Away seedling transplant plots, and at 30 points in Edge plots. External light conditions were measured simultaneously using a LI-COR 190SB quantum sensor attached to a LI-COR 10,000 data logger (LI-COR, Lincoln, NE) and within-plot measurements expressed as the percent of external photosynthetically active radiation (PAR). A second set of measurements was taken at Edges in July 1998 to indicate how light levels had changed after clipping was stopped. Since seedlings had by this time grown taller, sometimes overtopping competing vegetation, the 1998 measurements were adjusted for light received at the tops of plants using the difference between instantaneous measurements taken at the tops and bases of plants on a species by species basis, for 10 individuals per species per plot, 50 individuals per species per treatment.

Soil moisture was measured in seedling transplant plots three times in 1996 and once in 1998. We waited

for as long a period following rain as possible to obtain measurements when moisture would be most limiting. The 1996 measurements were taken 3–6 days after a rainfall event of >1 mm and the 1998 measurement was taken during drought conditions, 8 days following a rain. Five pooled soil samples were extracted from experimental plots to a depth of 10 cm from the top of mineral soil, weighed in the field, oven dried for 24 h at 100 °C, reweighed, and moisture content expressed gravimetrically. Soil moisture extraction curves were established for all soil samples using pressure plate extractors (Models CAT 1600 and 1500, Soil Moisture Equipment Company, Santa Barbara, CA) and gravimetric measures compared to moisture–tension relationships to assess water availability to plants. Leaf litter depth, measured from the litter surface to bare mineral soil, was determined at 10 randomly selected points in each seedling transplant plot.

2.7. Data analysis

Logistic regression was used to examine the effects of treatment and species on seed predation in the seed survival experiment (PROC LOGISTIC, SAS Institute, 1990). The logit of seed predation ($\log[\text{proportion of seeds removed/proportion remaining}]$) was the dependent variable with species, treatment, and the species \times treatment interaction as the independent variables. Design variables were created for each level of the independent variables since they were categorical (Hosmer and Lemeshow, 1989) and a posteriori Wald Chi-square tests used to indicate significant differences ($P \leq 0.05$) among levels. Logistic regression was also used to determine effects of species and treatment on the logit of germination ($\log[\text{proportion of seedlings emerging over the 2-year period/proportion of the estimated number of viable seed planted}]$) and the chance of establishing a first-year seedling in the seed sowing experiment. Due to the small number of seedlings that germinated, first year survivorship was expressed as a proportion of viable seed planted rather than seeds germinating. Mortality factors were not examined since many seedlings disappeared between survey dates leaving the cause of death unknown. *B. alleghaniensis* was excluded from these analyses due to very low germination.

Survival analysis (PROC LIFETEST in SAS) was used to assess the effect of treatment on second to

fourth year seedling survival for each species separately. This non-parametric test estimates the survival distribution functions of groups of subjects based on the survival times of each subject and tests for homogeneity in survival distributions among groups using a log-likelihood ratio test (SAS Institute, 1990). The test includes the effects of right-censored observations in which seedlings are withdrawn prior to termination of the experiment or remain alive at the end of the survey period, for which only a lower bound of survival time is known. Survival times were computed as the number of days between transplantation of seedlings and the survey date at which mortality was noted. The five sites per treatment were pooled in the analysis after first determining that survival patterns among them were similar (Hewitt, 1999). If results were significant ($P = 0.05$), two pairwise comparisons were made between (1) Away and Home treatments and (2) Away and Edge treatments. Pairwise comparisons were assessed at the $P = 0.01$ (family wise $P = 0.02$).

The effects of treatment and mortality agent on seedling mortality were assessed with logistic regression. Tests were run for each species separately with the logit of risk of mortality as the dependent variable, and treatment, agent, and the treatment \times agent interaction as independent variables. Mammals, desiccation, physical damage and unknown causes were grouped into a single “other” category, as cell sizes for these agents were small. Risk was calculated as the number of seedlings per treatment dying from a particular factor divided by “exposure time”, the number of weeks seedlings remained alive between transplantation in May 1996 and June 1998, summed across all seedlings per treatment (Agresti, 1990). Growth rates for 1996 and 1997 were compared between treatment and year using Model III, two factor ANOVA's with interaction (PROC GLM in SAS) with year treated as a repeated measure. Analyses were performed on each species separately since seedling height at transplantation varied significantly among species ($F = 506.2$, $MS = 2679.07$, $d.f. = 3$, $P < 0.0001$). Leaf number was compared between treatments using one-way ANOVA's in separate species analyses. For growth and leaf number analyses, species' mean values per site were treated as the data points to avoid pseudoreplication, and variables were log transformed prior to analysis. Analyses on environmental factors were performed on the four species

separately since some site locations differed between species. Mean leaf litter depth and percent external PAR were compared within and among treatments using Model III, hierarchical ANOVA's (PROC GLM in SAS), with site nested within treatment. Treatments were fixed effect and sites random effect variables. For PAR analyses, measurements taken at edges after clipping had ceased were treated as a fourth variable in the analysis. Mean percent soil moisture was compared between treatments and sample dates using repeat measure ANOVA's (PROC GLM in SAS). For ANOVA procedures, normality was assessed using normal probability plots of residuals from the fitted models and using the Shapiro–Wilk's test statistic. Tukey tests were used to indicate significant ($P < 0.05$) differences between means, except in PAR analyses for which a least squares means procedure appropriate for unbalanced designs was employed. Percent values were arcsine square root transformed prior to analysis.

3. Results

3.1. Environmental conditions

Light levels were comparable between Home and Away treatments and significantly higher at Edges ($F > 18.57$, $P < 0.0001$, $d.f. = 3$, all species). Fig. 2 presents data for *F. grandifolia*, but results were the same for all species' plot environments. Light varied significantly among sites within treatment ($F = 3.35$ – 4.42 , $P < 0.0001$, $d.f. = 16$, all species), but only for the Edge treatment as might be expected given differences in aspect and foliage character among edges. Ground level light measured at Edges during the clipping treatment (in 1996 and 1997) was not significantly different from light levels at the tops of plants in 1998 after clipping was stopped indicating that seedlings had overtopped competing species and were continuing to receive increased light levels at edges.

Mean soil moisture was significantly lower at Edge sites than Home and Away sites, as expected given the greater exposure and illumination at edges (Fig. 3) ($F = 16.39$, $MS = 785.06$, $P < 0.0004$, $d.f. = 2$). However, soil moisture was also lower in Away than Home sites, likely due to the coarser-grained sandy soils in the north part of the study area where most

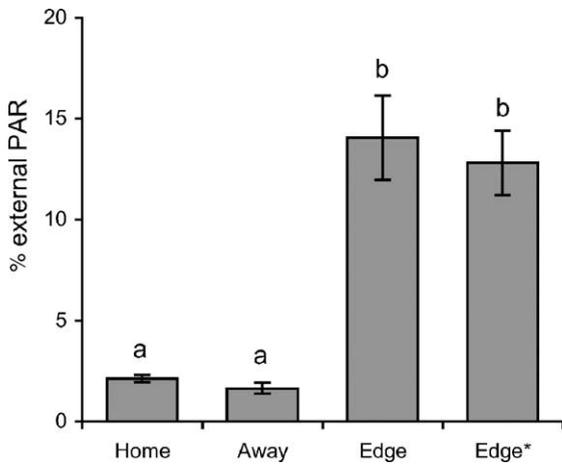


Fig. 2. Mean (\pm S.E.) percent external photosynthetically active radiation in experimental treatments for *F. grandifolia*. Edge 2 refers to measurements taken at the tops of seedlings after clipping ceased in 1998. Values with the same letter are not significantly different.

Away sites were situated (Fig. 1b). Nevertheless, soil moisture tension data indicated that moisture had not fallen below wilting point in any of the treatment sites on the four sample dates, and had fallen below field capacity (0.3 bar pressure) in only one or two sites per Home and Away treatment on one or two sample dates (Home treatment: HC7 on 16/07/98; Away treatment:

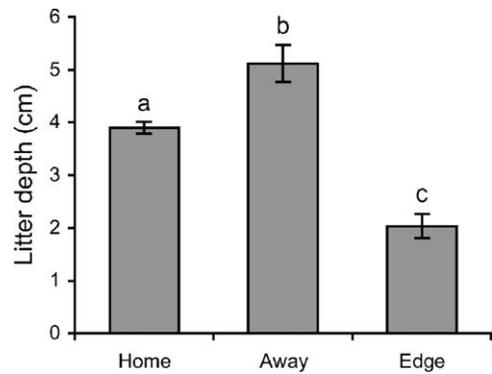


Fig. 4. Mean (\pm S.E.) leaf litter depth in experimental treatments for *F. grandifolia*. Values for other study species were comparable. Values with the same letter are not significantly different.

A2 on 29/07/96, A5 on 6/07/96 and 16/07/98) (Hewitt, 1999). Mean leaf litter depth was significantly lower in Edge than Home and Away treatments, as expected from the sparser tree canopy at edges, but was also greater in the Away than Home treatment ($F > 36.46$, $P < 0.0001$, d.f. = 2, all species) (Fig. 4).

3.2. Seed survival

Seed predation rates differed significantly among species ($G = 96.18$, $P < 0.0001$, d.f. = 2) but not

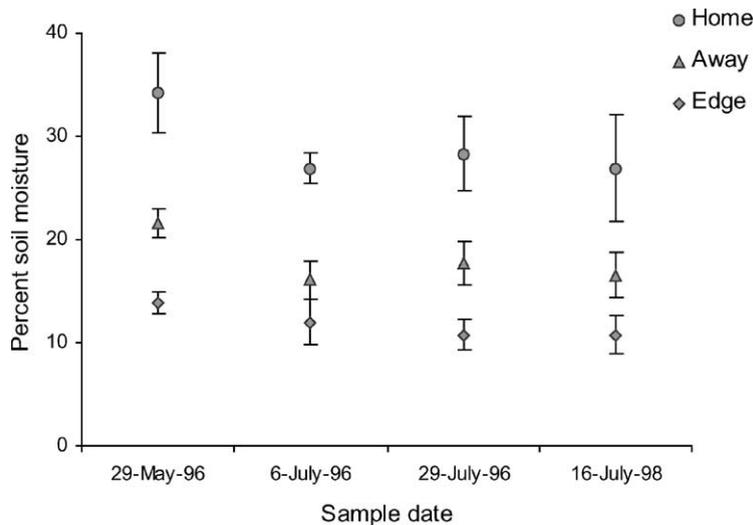


Fig. 3. Mean (\pm S.E.) percent soil moisture in experimental treatments by survey date for *F. grandifolia*. Values for other study species were comparable.

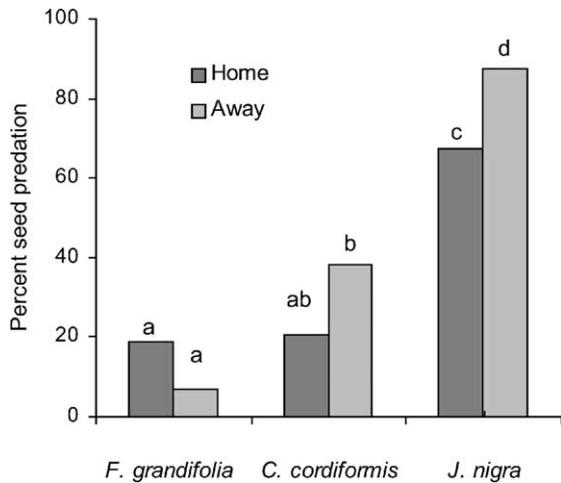


Fig. 5. Percent seed predation for *F. grandifolia*, *C. cordiformis* and *J. nigra* in Home and Away treatments. Values with the same letter are not significantly different ($P > 0.05$) using Wald Chi-square tests.

treatments ($G = 3.57$, $P > 0.05$, d.f. = 1) and the interaction was significant ($G = 9.37$, $P < 0.001$, d.f. = 2), prompting single-species analyses. Between-treatment differences were present for *J. nigra* only, with predation in Away > Home (Fig. 5). Predation was greatest for *J. nigra*, the largest-seeded species, and lowest for *F. grandifolia*, the smallest-seeded.

3.3. Seed germination and first-year seedling establishment

Germination of *F. grandifolia*, *C. cordiformis* and *J. nigra* differed significantly between species ($G = 62.09$, $P < 0.0001$, d.f. = 2) and treatment ($G = 10.93$, $P < 0.005$, d.f. = 2) and the interaction was significant ($G = 68.45$, $P < 0.0001$, d.f. = 4) (Fig. 6). The Escape hypothesis was supported only for *C. cordiformis*, and the Edge hypothesis only for *J. nigra*. Patterns for *F. grandifolia* were opposite to those predicted under either hypothesis. Germination of *B. alleghaniensis*, though not analyzed statistically, was low in all treatments. The chance of a species' seed producing a first-year seedling as a proportion of viable seed planted differed significantly among species ($G = 199.43$, $P < 0.0001$, d.f. = 2) and treatment ($G = 40.89$, $P < 0.0001$, d.f. = 2) with interaction ($G = 25.5$, $P < 0.0001$, d.f. = 4). Patterns were similar to those observed at germination (Fig. 7).

3.4. Second to fourth year seedling survival

The repellent used to prevent mammal predation was not entirely effective, as some seedlings in protected plots were predated. However, the frequency of mammal attack was low in both the mammal protected and unprotected plots and there was no significant difference between them ($T < 1.47$, $P > 0.18$, all

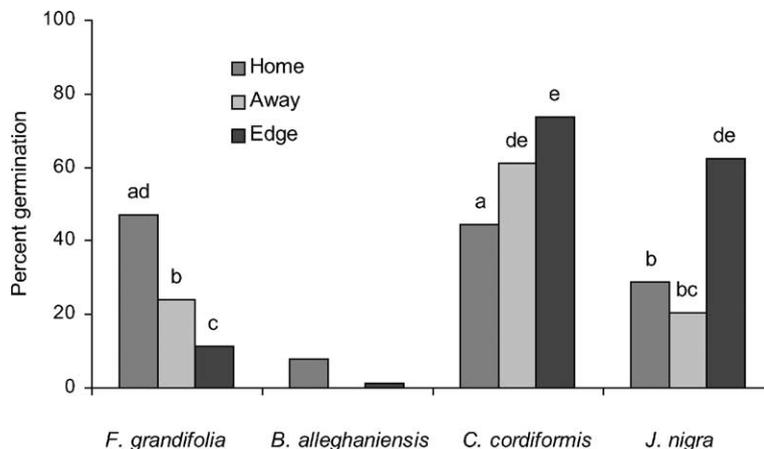


Fig. 6. Percent seed germination of study species in Home, Away and Edge treatments. Values with the same letter(s) are not significantly different. *B. alleghaniensis* was not included in the analyses due to the small number of events.

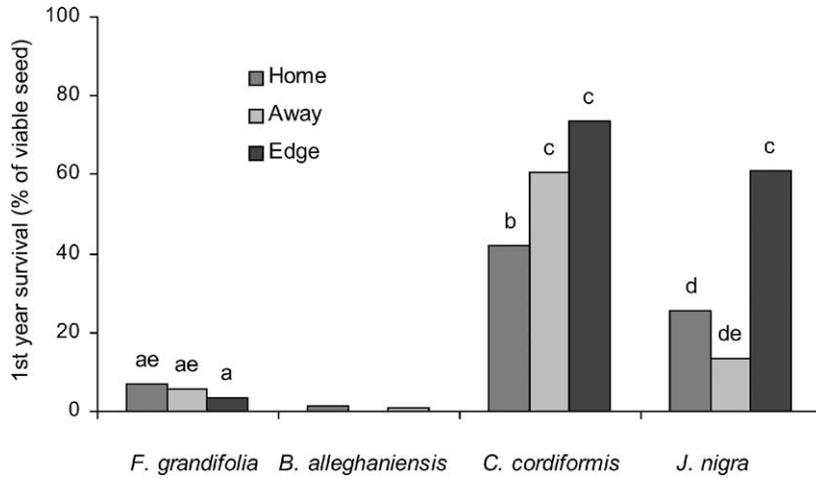


Fig. 7. Seedling survival to the end of one growing season expressed as a percent of the viable seed planted. Values with the same letter(s) are not significantly different. *B. alleghaniensis* was not included in the analyses.

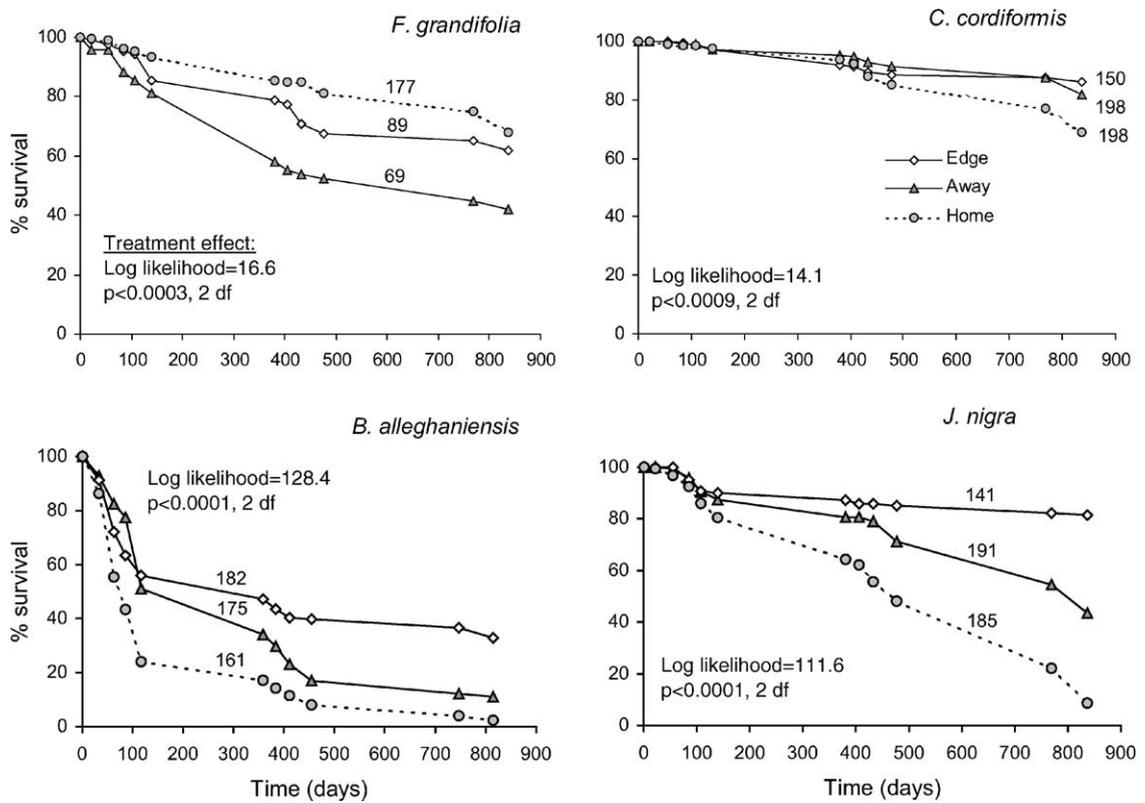


Fig. 8. Percent survival of seedling transplants by treatment and survey date for the 1996–1998 growing seasons. Day 0 was 12 May 1996 for all species except *B. alleghaniensis*, for which day 0 was 2 June 1996. Seedlings were 1-year-old at the start of the experiment. Number of seedlings per treatment at the start of the experiment is shown adjacent to curves.

three species), so seedlings from protected and unprotected Home and Away plots were combined to increase sample sizes (40 seedlings per species, 200 per treatment). Survival times were greater in Away than Home treatments for *B. alleghaniensis*, *C. cordiformis*, and *J. nigra*, in keeping with the Escape hypothesis, and in Edge than Away treatments for *B. alleghaniensis*, *F. grandifolia* and *J. nigra*, in keeping with the Edge hypothesis (Fig. 8). Survival from the second to fourth year was greatest for *C.*

cordiformis (>64%, all treatments) and lowest for *B. alleghaniensis* (<38%). *J. nigra* survival was highly variable depending on treatment (Edge: >80%; Away: 42%; Home: <10%).

Pathogens were the major cause of *J. nigra* mortality in all sites and of *C. cordiformis* mortality in Home sites, while unknown factors accounted for a large proportion of deaths among *F. grandifolia* and *B. alleghaniensis*, followed by insects and/or desiccation (Fig. 9). Physical damage and mammal herbivory

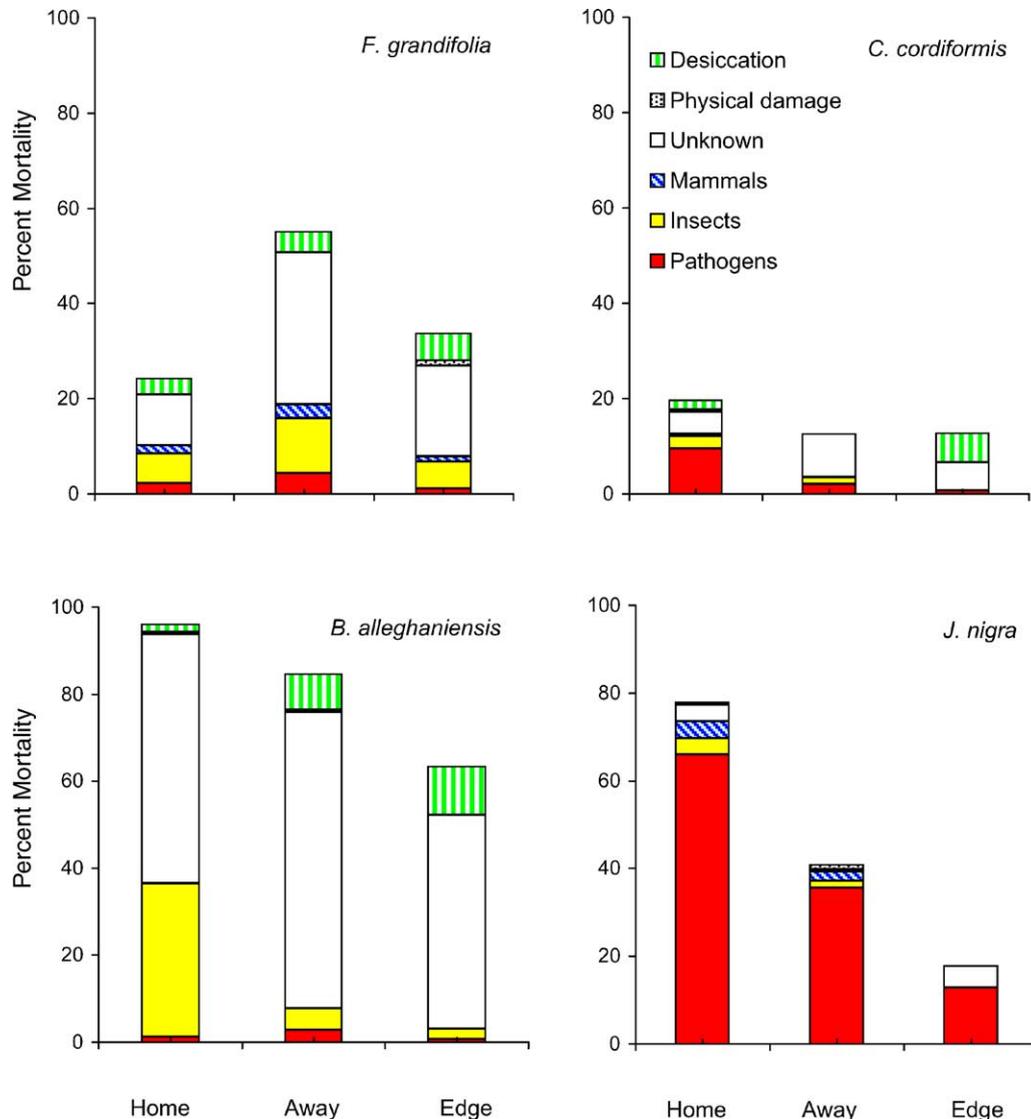


Fig. 9. Percent seedling mortality by different agents in each experimental treatment for the period May 1996–June 1998.

Table 2
Risk of seedling mortality by adverse agents in each experimental treatment^a

Species	Agent	Risk			G		
		Home	Away	Edge	Treatment	Agent	Interaction
<i>J. nigra</i>	Pathogens a	0.012 a	0.0045 b	0.0014 c	130.40***	259.03***	6.09 N.S. ^b
	Insects c	0.00077	0.0002	0			
	Other b	0.0013	0.00093	0.00052			
<i>C. cordiformis</i>	Pathogens	0.001 a	0.0002 b	0 b	8.59*	41.29***	17.20***
	Insects	0.00026 b	0.00015 b	0.000067 b			
	Other	0.0011 a	0.00089 a	0.0012 a			
<i>F. grandifolia</i>	Pathogens c	0.00025 a	0.00068 b	0.00014 a	26.09***	74.67***	2.27 N.S.
	Insects b	0.00068	0.0018	0.00069			
	Other a	0.0017	0.0061	0.0033			
<i>B. alleghaniensis</i>	Pathogens	0.00063 e	0.00086 de	0.00013 e	210.53***	474.12***	74.85***
	Insects	0.02 c	0.0015 d	0.00059 de			
	Other	0.033 c	0.025 b	0.012 a			

^a “Other” includes mammal attack, desiccation, physical damage, and unknown causes of mortality. Values with the same letter are not significantly different. In models without interaction, treatment comparisons are shown in the first row of values, and agent comparisons are shown in columns next to agent labels. *G* is the log-likelihood ratio test statistic.

^b Not significant.

* Significant at $P < 0.05$.

*** Significant at $P < 0.0001$.

were minor sources for all species. The main insect predators were moth or butterfly larvae. Three of the four types of pathogens detected on seedlings were host-specific: *Microstroma juglandis* and *Gnomonia leptostyla*, which attacked *J. nigra*, and an unidentified leaf spot on *C. cordiformis*. *G. leptostyla* and the leaf spot produced severe damage and were most frequent in Home sites. The non-host-specific pathogen, *Microsphaera penicillata*, attacked both *J. nigra* and *C. cordiformis* and was equally frequent in Home and Away treatments, but infrequent at Edges (Hewitt, 1999).

J. nigra mortality by pathogens, insects and other (mammals, desiccation, physical damage and unknown) agents supported the Escape and Edge hypotheses (Home > Away > Edge, Table 2). For *C. cordiformis*, patterns of pathogen mortality supported the Escape hypothesis. Rates of insect mortality were also greater in the Home than Away treatment, but not significantly. *F. grandifolia* mortality by pathogens, insects, and other agents supported the Edge hypothesis, but was contrary to predictions under the Escape hypothesis (Away > Home). For *B. alleghaniensis*, rates of insect mortality supported the Escape

hypothesis. Responses for this species are difficult to evaluate, however, because of the high proportion of deaths due to unknown factors, which may have concealed effects of insects and pathogens (Fig. 9).

Growth was greater at the Edge than Away treatment for all species except *J. nigra* (Fig. 10). Leaf number was greater at the Edge than Away treatment for all species, but the difference was not significant for *B. alleghaniensis* or *F. grandifolia* (Fig. 11).

3.5. Cumulative percent survival to fourth year seedling establishment

Survival of the four species was low in the early stages of seedling establishment across all treatments, and improved markedly thereafter (Fig. 12). Probabilities of fourth year seedling establishment were very low for *B. alleghaniensis*, *F. grandifolia*, and *J. nigra* at fewer than 5% in well-illuminated microsites (0.01, 1.4 and 4.6% for the species, respectively), and a fraction of a percent in shady forest interiors (<0.002, <1.0, <0.5, respectively). *C. cordiformis* had relatively high probabilities of producing a fourth year seedling (Home: 20.7%; Away: 27.2%; Edge: 34.3%). Survival to the

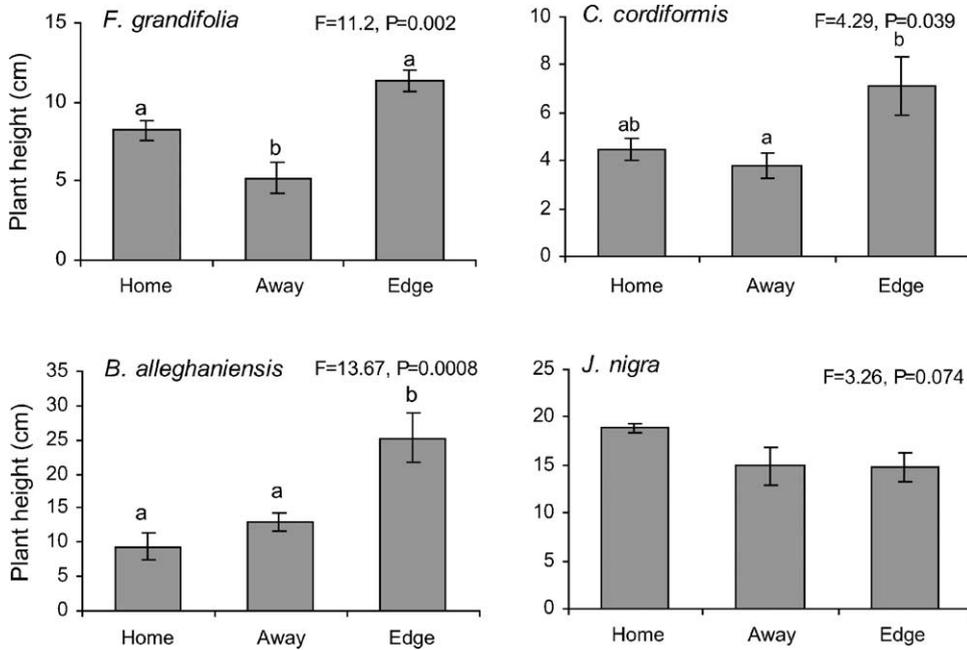


Fig. 10. Mean (\pm S.E.) change in height (May 1996–August 1997) for seedling transplants. Means were calculated from plot means ($n = 5$). Values with the same letter are not significantly different ($P > 0.05$).

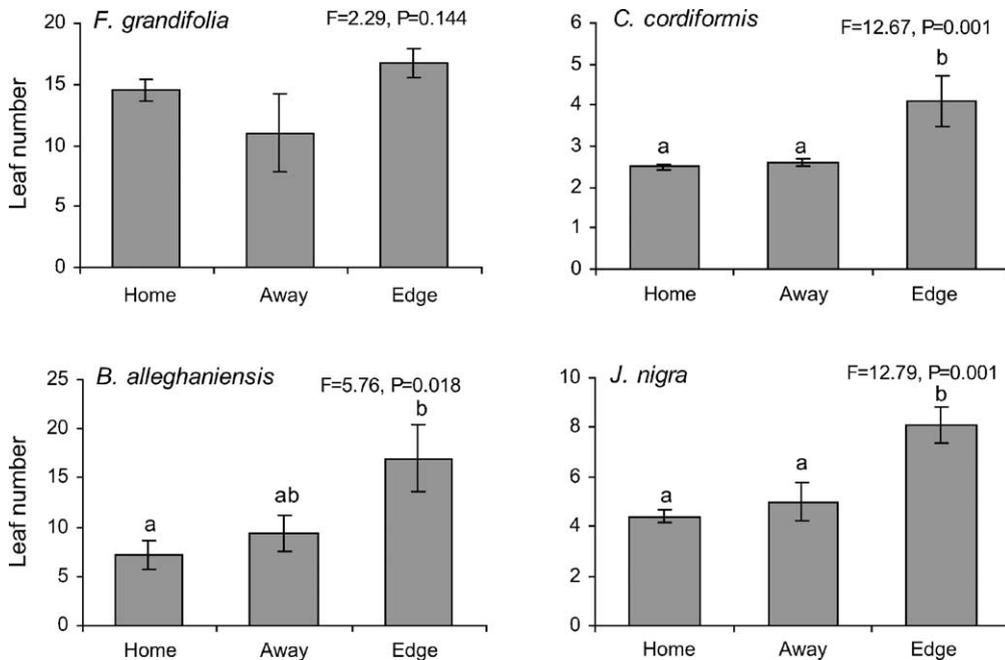


Fig. 11. Leaf number (mean \pm S.E.) for seedling transplants. Means were calculated from plot means ($n = 5$). Values with the same letter are not significantly different ($P > 0.05$).

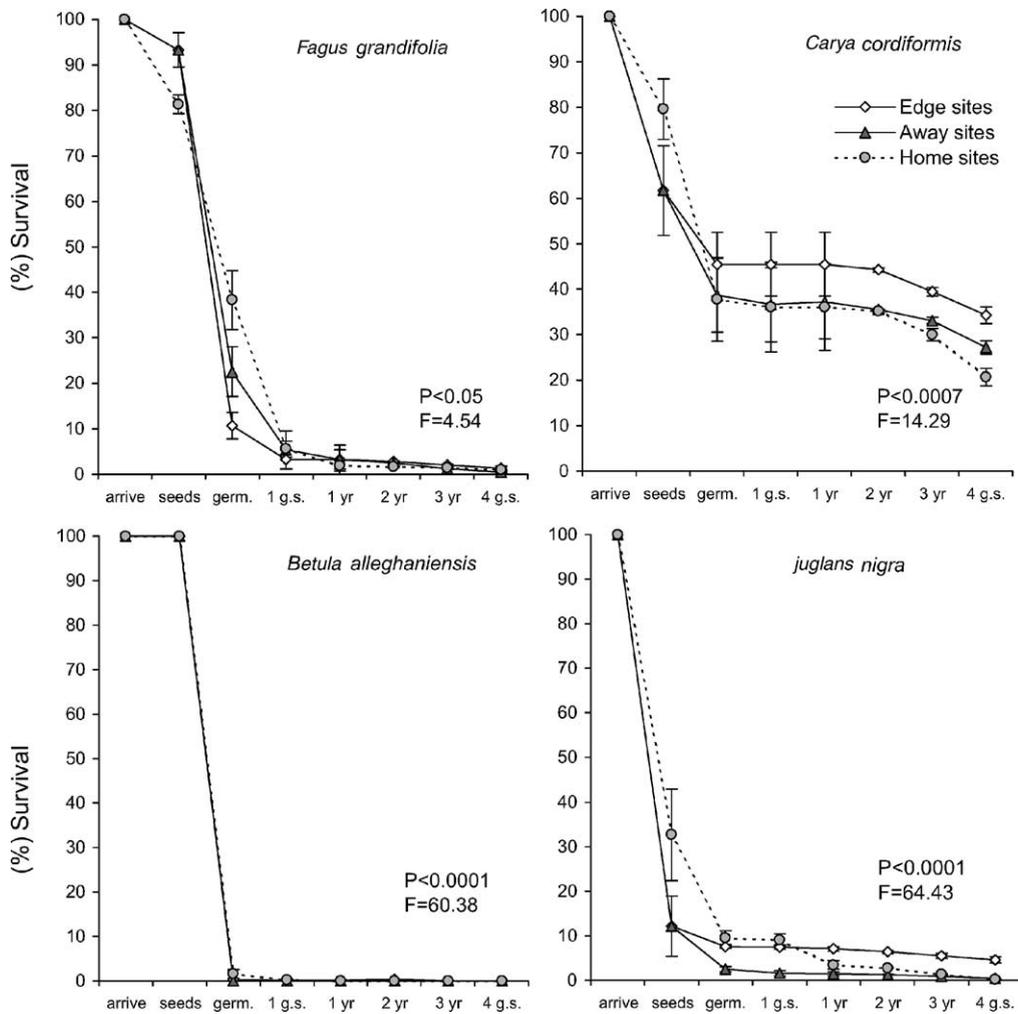


Fig. 12. Cumulative percent survival from seed arrival to the end of a fourth growing season. Stages are – arrive: immediate post-dispersal, seeds; germ.: germination; 1 g.s.: seedlings at the end of one growing season; 1 yr: seedlings at the end of the 1 yr; 2 yr: seedlings at the end of 2 yr; 3 yr: at the end of 3 yr; 4 g.s.: seedlings at the end of the four growing seasons. Invertebrate seed mortality, if any, is included in the germination stage. Values for germination and 2-year survival are calculated using treatment means for the previous stage in the seed predation and germination – first year survivorship experiments. Seed predation values for the Away treatment were used for Edges, assuming that values in canopy gaps, for which Edges were facsimiles, would be comparable to closed canopy sites. Results for ANOVA's on arcsine square root transformed % survivorship at the end of the fourth growing season are indicated. In analyses on *B. alleghaniensis*, 0.1 was added to zero values at the end of the germination – first year survivorship experiment. Vertical bars indicate standard error.

end of the fourth growing season was significantly improved by being a colonizing individual for *C. cordiformis* and *B. alleghaniensis*, though the difference between Home and Away treatments was less than 0.01% in the latter. Survival of all species was significantly higher at edges than the forest interiors of uncolonized woodlots, though the difference was less than 1% for *F. grandifolia* and *B. alleghaniensis*.

4. Discussion

The present study indicates the colonization abilities of four eastern deciduous forest tree species and provides evidence for the importance of two influencing factors, spatial separation from natural enemies and arrival in well-illuminated micro-sites. We first assess the degree to which experimental plot environ-

ments satisfied the assumptions of the experiment, then discuss the results of the hypothesis testing and how species responses were related to seed size and developmental stage. Finally, we evaluate the relationship between seed arrival and establishment and its significance to inter-fragment tree colonization.

4.1. Experimental plot environments

The experimental plot environments satisfied the major assumptions regarding light availability for the Edge hypothesis and presence of conspecifics for the Escape hypothesis. However, the lower soil moisture and greater litter depth in Away sites relative to Home were unintended. Soil moisture differences likely resulted from the coarser soil textures in the north part of the study area where uncolonized woodlots were situated. Nevertheless, these soils did not fall below wilting point, and only infrequently fell below field capacity, even during drought conditions when samples were taken. Furthermore, seedlings had comparable rates of desiccation among Home and Away treatments indicating that they were not exposed to moisture shortages in uncolonized woodlots relative to those in colonized ones. Other soil properties associated with textural differences such as acidity, nutrient retention, and soil microorganisms might be expected to make conditions more favorable for survival and growth in the Home sites than Away. The finer textured soils of the Home sites would tend to be richer in organic matter and nutrients and less acidic (Presant and Acton, 1984). Yet, survival was greater in Away than Home sites for all species except *F. grandifolia*. *F. grandifolia* is known to grow best in deep soils rich in organic matter (Burns and Honkala, 1990) and tends to be more abundant in parts of the study area with finer grained soils (pers. obs.; Varga, 1985), so its greater survival in Home sites may have been a response to soil properties. Of particular relevance to this study, the moister conditions in Home sites might have promoted the growth of fungal pathogens on seedlings, and this would exaggerate pathogen effects predicted under the Escape hypothesis. However, pathogens were not infrequent on seedlings in Away sites. For the two species having lower rates of seedling mortality by pathogens in Away sites, *J. nigra* and *C. cordiformis*, the types of pathogens concerned tended to be host-specific, suggesting that spatial

constraints rather than humidity affected their distributions.

The deep leaf litter in Away sites may be attributed to the abundance of *Quercus* species (*Q. alba*, *Q. rubra*), whose litter is relatively slow to decompose (Burns and Honkala, 1990). A possible effect of deep leaf litter is to inhibit seed germination or lead to physical damage of newly emerged seedlings from litterfall (Facelli and Pickett, 1991; Scariot, 2001). However, germination and first year survivorship was lower in Away sites only for *F. grandifolia*, and for this species, soil differences are believed to have been influences that are more significant.

A final consideration relates to the location of many of the Home sites in a large continuous forest, compared to the forest fragments containing Away sites. However, the fragments used in the present study, with the exception of site A4, were relatively large (>10 ha) and the sites within them were at least 50 m from a forest edge. Moreover, the literature from tropical environments suggests that conditions in a large continuous fragment will be superior for seedling establishment and survival of most species due to the absence of edge effects (Murcia, 1995; Benitez-Malvido, 1998; Scariot, 2001) or to lower concentrations of seed predators (Santos and Tellería, 1997, but see Wong et al., 1998). Yet our study indicated no consistent difference in seed survival between Home and Away sites for the species and that young seedling survival was generally better in the isolated fragments (see below). We therefore assume that the presence or absence of conspecifics was an important factor in survival differences between the Home and Away treatments.

4.2. Species responses to treatments

With the exception of possible moisture effects on pathogens, the problems of experimental control would be expected to make conditions generally less favorable in uncolonized woodlots relative to colonized woodlots. Yet survival tended to be greater in the former, with the increased survival occurring mainly during later seedling establishment, from the second to fourth year. This suggests that there were advantages to establishing in the isolated fragments relative to the Home sites and, as suggested earlier, we attribute this to the lack of members of the species and their

host-specific predators in the former, as proposed by the Escape hypothesis. This is supported by the lower seedling mortality by fungal pathogens and insects in Away relative to sites. The other possible explanation relates to the better-drained soils in the north part of the study area where fragments were. This factor might contribute to the lower pathogen and insect populations. However, the soil moisture tensions were comparable among sites suggesting that moisture availability to organisms was similar. Further, the pathogens responsible for differential mortality tended to be host-specific and highly lethal, providing further evidence that separation from predator and pathogen concentrations in fragments unoccupied by the species contributed to greater survival. The hypothesis that sites with better illumination would promote colonization was also supported among second to fourth year seedlings. There was better performance at edges for all species and lower mortality by pathogens for *J. nigra* and *F. grandifolia* at edges compared to forest interiors. This indicates that sites such as edges recently cleared of shrubby vegetation may provide unique opportunities for tree establishment and colonization. It also suggests that large gaps may be important sites for fragment colonization, though this hypothesis needs to be investigated for gaps specifically. The four species investigated in this study spanned the range of shade-tolerance, suggesting that well-lit sites may provide colonization benefits to shade-tolerant and shade-intolerant species alike.

Prior to the second year, responses were not consistently related to treatment. Rather, responses seemed to be related to species-specific attributes. At the seed stage, predation of one species, *J. nigra*, differed between Home and Away treatments, being greater in woodlots lacking the species. As might be expected, rodent populations and the foraging efforts of these generalist seed predators were probably influenced by the presence of other prey species such as *Quercus*, *Acer* and *Carya* spp. (Smith and Follmer, 1972; Thompson and Thompson, 1980) which occurred throughout the system in uncolonized and colonized woodlots alike. *J. nigra* seeds are a preferred food item of squirrels in eastern deciduous forests (Smith and Follmer, 1972) and given the presence of squirrels throughout the system, the scarcity of *J. nigra* seeds in Away sites combined with a strong smell to facilitate detection, may have promoted predation, a

trend consistent with the predator satiation hypothesis (Janzen, 1971). Other studies in fragmented systems have indicated that isolated fragments produce greater rodent predation compared to continuous forest (Scariot, 2001). However, in this case we would expect the other two species to have experienced greater predation rates in Away sites also. It is possible that the difference in our findings relates to the relatively large size of fragments used in the study.

During germination, only *C. cordiformis* patterns supported the Escape hypothesis and only *J. nigra* and *C. cordiformis* supported the Edge hypothesis, with the latter having a very weak response. Patterns of first-year seedling survival were similar to those observed during germination. This may reflect the tendency for species to be sensitive to fine-scale features in the environment during germination and early seedling establishment and to require very precise sets of conditions to break dormancy in a highly species-specific manner (Harper, 1977; Angevine and Chabot, 1979). The species may have been responding to substrate conditions rather than larger scale factors associated with treatment effects. For example, *F. grandifolia* grows best in mesic, organic matter-rich soils, and had the greatest germination rates in the Home sites, followed by the drier Away sites and finally the exposed and even drier Edge sites. *C. cordiformis*, a species tolerant of drier, sandy soils, had the opposite response (Burns and Honkala, 1990). The small between-treatment differences in *B. alleghaniensis* germination may reflect the quality of the logs in which seeds were planted rather than treatment, since germination on dead-wood is highly sensitive to the level of decay of the wood. Attempts were made to choose logs of similar quality at all sites, but there may have been variation in log quality between treatments due to more limited availability of highly decayed wood in the privately owned and probably harvested uncolonized woodlots.

4.3. Relationship between seed size and survival of seeds and young seedlings

While survival of seeds and young seedlings was not obviously influenced by the species' exoticism or location with respect to canopy openings, neither was it entirely haphazard, but varied according to species attributes such as seed size. Seed survival

was inversely related to seed mass, though the association was somewhat weak. Predation in uncolonized woodlots was 88% for *J. nigra*, 38% for *C. cordiformis*, and 6.7% for *F. grandifolia*. The smallest seeded species, *B. alleghaniensis*, though not tested, may be assumed to be last on this list according to information in the literature (Burns and Honkala, 1990) and observations made by the researcher during the experiment. This relationship is likely a function of the amount of nutrition contained within the seed (Crawley, 1992), although the particularly heavy predation of *J. nigra* seeds may be influenced by ease of detection and food quality as well food quantity. Germination and first-year seedling survival were also related to seed size, though in the opposite direction, being higher among larger-seeded species (*C. cordiformis* > *J. nigra* > *F. grandifolia* > *B. alleghaniensis*). A seed sowing experiment on 12 species in the study system, including these four, corroborated this finding, indicating a weak positive relationship ($P = 0.0097$; $R^2 = 0.50$) between log seed mass and log survival to the end of the second growing season (Hewitt and Kellman, 2002a).

These findings indicate a stage-specific pattern of vulnerability during colonization in relation to seed-size. Vulnerability of larger seeded species, *C. cordiformis* and *J. nigra* was concentrated at the seed and germination stages due to heavy rodent predation in the former and failure to emerge in the latter, while the greatest risks among smaller seeded species, *B. alleghaniensis* and *F. grandifolia*, occurred during emergence and the first year. These seed size relationships produced minimal interspecific differences in survivorship to the fourth year, however, as they tended to cancel each other out across stages. High rates of seed survival among the two smaller seeded species were offset by low germination and first-year seedling establishment, while the high rates of germination or first-year seedling survival among the larger seeded species just compensated for relatively low survival at the seed stage.

4.4. Importance of escape from natural enemies and gaps to fourth year establishment

While establishment in unoccupied woodlots and well-lit sites improved survival of post-second-year seedlings, the overall effect was small due to the tiny

percentage of seedlings reaching the second year when benefits became operative. *C. cordiformis* had unusually high second year survival in uncolonized woodlots (>35%), but the other three species had fewer than 2.5% of seedlings passing from the first to the second year in uncolonized woodlot interiors, and under 2.8% for *F. grandifolia* and *B. alleghaniensis* at edges, 6.4% for *J. nigra* (Fig. 12). Thus, there remained only a small proportion of seedlings on which the post-second-year advantages could operate, and by the end of the fourth year, the numeric advantages to being exotic or growing in well-lit sites were marginal. Only two species had significantly greater survival in Away than Home sites, and for one of these the difference was less than 1%. The effect of well-lit microsites was somewhat more pronounced, producing significantly greater fourth year survival than forest interiors for all species. For two of these, *C. cordiformis* and *J. nigra*, the difference was relatively substantial at >4%. However, for the other two, it was minor at just a fraction of a percent.

4.5. Link between seed arrival and seedling establishment

The low survivorship of seeds and small seedlings and resulting low probabilities of fourth year seedling establishment implies that spontaneous colonization of a fragment is really contingent upon a large supply of incoming seed. To produce just one fourth year seedling in an unoccupied woodlot, *F. grandifolia*, *J. nigra*, and *B. alleghaniensis* require >200, >230, and >10,000 incoming seeds into shady microsites for the species respectively, or >70, >20, and >1000 seeds into well-illuminated sites. *C. cordiformis* would need much fewer; under five seeds in both site types. Yet extraneous seed rain into isolated fragments is likely to be rare and insufficient to meet these demands. A previous study of medium to long-distance dispersal for these tree species indicated that, while dispersal was relatively frequent over distances of 50–75 m, only one of the study species, *F. grandifolia*, showed evidence of dispersal over distances of 150–175 m over a 4–11-year measurement period (Hewitt, 1999; Hewitt and Kellman, 2002b). In relation to the findings of the present study, dispersal represents a constraint on colonization of even those species with high probabilities of producing a seedling from extraneous seed,

such as *C. cordiformis*: 34% survival of zero seeds arriving in a fragment amounts to no migration.

5. Conclusions and management recommendations

This study suggests that the four tree species treated will have low chances of seedling establishment and colonization in forest fragments. In general, seedlings were most vulnerable during the seed and early (first to second year) seedling stages. *J. nigra* and *C. cordiformis* mortality was largely due to rodent seed predation or failure to emerge and pathogen attack on seedlings, though pathogen mortality was considerably reduced by establishment in uncolonized woodlot interiors and edges relative to colonized. Failure of seeds to germinate and seedling mortality by insects, desiccation and unknown factors explained most *B. alleghaniensis* and *F. grandifolia* mortality, and rates of survival for these two species were generally low in all treatments. *C. cordiformis* had relatively high rates of fourth year seedling establishment compared to the other species, with increased survival in uncolonized fragment interiors and edges. However, poor inter-fragment dispersal for *C. cordiformis* greatly reduces its chances of colonizing new fragments.

The low early seedling survivorship measured here combined with very infrequent dispersal between isolated fragments (Hewitt and Kellman, 2002b) suggest that local extinctions in fragmented forests may fail to be compensated for by inter-patch colonization, leading to regional extinctions. Species reintroductions may provide a short-term solution to this dilemma, and based on our findings, the following recommendations can be made. Seedling transplantation is recommended over seed sowing. Lamb et al. (1997) report that direct seeding is only more efficient than transplantation if greater than 1% of sown seeds are expected to survive, a condition which only one of four study species satisfied. In addition, transplantation of first- or second-year seedlings would avoid the risky seed—first-year seedling period, and bring colonizing individuals to a stage at which benefits associated with the Escape and Edge hypotheses become important. Transplantation into sites of high-illumination such as edges may further improve chances of success. While we focused on edges, the same benefits

of increased light may be expected to exist in canopy gaps, and these should be investigated for their potential to facilitate colonization.

However, seedling introductions cannot substitute for vigilance in conservation. Reintroductions are costly and labor intensive, requiring careful planning and an ongoing commitment at a time when government support to forest authorities and conservation agencies in North America is dwindling. Changes in land ownership, conservation mandates and personnel, and in societal values over time make it unlikely that such efforts would be viable over the long term. Furthermore, fragmented forests may be environmentally inhospitable in ways that prevent successful reintroductions, for example, through lowered water tables, desiccating conditions, and pesticide effects on plants and insect pollinators. In the event of climate change, widespread local extinctions in fragmented landscapes due to shifting geographic ranges combined with migration barriers (Davis and Zabinski, 1992) may make a species-by-species conservation approach unmanageable. Therefore, this research demonstrates the need to prevent further unnecessary habitat loss.

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