Forest regeneration in 1998 ice storm gaps In an old-growth hemlock forest in Vermont

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Abstract

Natural disturbances influence forest regeneration processes and have often been the primary cause of historical compositional change (Henry and Swan 1974). The early stages of forest regeneration in gaps may be important for the later forest composition. This study examined regeneration in the first 4 growing seasons of gaps created by the 1998 ice storm in the Battell Research Forest (BRF) in Vermont. By 4 years after the ice storm, seedlings in the gaps had already experienced considerable mortality, as evidenced by decreases in stem densities. Mortality rates were higher for shade intolerant species than for either species of intermediate tolerance or tolerant species. Nearby intact forest sites had lower densities of seedlings but higher species richness than the gaps. The BRF may be experiencing a change in disturbance regime from fire to wind and a corresponding change from historical hemlock and pine dominance to an increasing dominance by northern hardwood species as suggested by the capture of gaps by hardwoods after the Great Appalachian Windstorm of 1950 (Mann et al., unpublished). Four years after the 1998 ice storm, half of gaps showed greater importance of hemlock than northern hardwood species, collectively, thus overall hemlock dominance of the forest does not seem to be immediately threatened. However, the small size of the BRF may make it highly susceptible to influence by the surrounding hardwood stands. Furthermore, there are a number of plausible scenarios that could shift the balance between hemlock and northern hardwood species in the Battell Research Forest.

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Introduction

A natural disturbance is a discrete event that removes biomass and/or kills individuals, thereby providing the opportunity for the establishment of new individuals (Sousa 1984). Disturbances can disrupt ecosystems, communities, and population structure as well as change abiotic factors, such as available resources and substrate (White and Pickett 1985). Certain forest communities and/or regions tend to be characterized by particular types of disturbances; this pattern represents a disturbance regime. Fire, windthrow, ice storm, avalanche, and volcanic eruption are only some examples of disturbance types.

Different disturbance regimes will affect communities and environmental factors in different ways. The effect of an individual disturbance depends largely on its magnitude, which is a combination of its intensity and the severity of damage caused. There is a continuum of possible damage, ranging from some biomass removed but no individuals killed to complete biomass and soil removal (Oliver and Larson 1990). For example, a very severe fire in the history of a New Hampshire forest initiated a forest completely different in composition than the previous one (Henry and Swan 1974). The severity of a disturbance will most likely affect which regeneration strategy will succeed in the disturbed area by affecting propagule availability (Runkle 1985). It will also influence the recovery time of a forest. The size of the area disturbed is another major factor. Forest-wide fires characterize the communities of the Great Lakes region (Frelich and Lorimer 1991) while the falling of individual trees characterizes tropical forests (Pickett 1983). However, even very small disturbances often result in recruitment of new individuals, and thus provide for the important processes of forest regeneration (Runkle 1982). The temporal scale of disturbance also influences its effect on a forest. The episodic, often unpredictable, nature of disturbance lends to the rapid and dramatic effects that may result in forest composition changes (Foster 1988a). Both average disturbance rate (the rate of tree death) and natural rotation times (how long until canopy replacement after disturbance) are quite similar for considerably different forest types with different disturbance regimes (Runkle 1982). Thus the temporal and spatial distribution and severity of disturbance may be more important determinants of overall effects on the landscape.

The effect of a disturbance stems not only from its severity and scale but also from the susceptibility of the stand to the particular disturbance type (White 1979). The forest structure influences what effect the disturbance has, which in turn influences the resulting stand structure; thus, disturbances are integrated into community dynamics. The 1938 hurricane differentially damaged stands of differing age structure and composition (hardwoods or conifers), leading to differences in resulting site conditions and subsequent vegetation development (Foster 1988b). Temporal and spatial distributions of disturbance also affect a forest's future susceptibility to disturbance. For example, stands increase in susceptibility with age (Foster 1988b; Runkle 1985), but trees along the edge of previously disturbed site are more vulnerable to wind disturbance due to the abrupt height differences (Foster 1988a). In characterizing a disturbance regime, therefore, the important factors are not only spatial extent, intensity, and return interval (Foster 1988a) but community type, structure, and history.

In the Pisgah Forest of New Hampshire, disturbances have been the primary cause of compositional change (Henry and Swan 1974). Natural disturbances contribute to forest regeneration by providing opportunities for recruitment, making available specific regeneration niches for species (e.g. Canham and Marks 1985; Clark 1991b; Foster 1988a; Foster 1988b), and allowing for the persistence of rare species (Poulson and Platt 1989). Over the long-term, disturbances cause much of the spatial and temporal heterogeneity in natural communities as well as influence the evolution of life histories for species (Sousa 1984).

Several kinds of disturbances create gaps, which are openings of the forest canopy created by fallen trees. Some gaps are small enough to be closed by lateral growth of remaining canopy trees while intermediate and large gaps are closed by the growth of recruits (Hibbs 1982). The early stages of colonization of a newly formed gap may be important for its later composition. The colonizing individuals can come from three sources: the seed bank, newly dispersed seeds, and advance regeneration (suppressed seedlings and saplings that were present in the understory before the disturbance) (Canham and Marks 1985). The overall establishment period seems to be brief (1-5 years following the disturbance event) (Canham and Marks 1985). The initial floristics pattern, which characterizes invasion after a disturbance, predicts that most species that later dominate in gaps (called gap capture if they reach the canopy) would have been present since shortly after the disturbance event (Oliver and Larson 1990).

After this burst of new establishment, competition for resources results in mortality, and thus reductions of stem density. Peterson and Pickett (1995) found that the rate of seedling establishment began to decrease after the second year following the disturbance. Similarly, Peterson et al. (1990) documented decreased levels of total plant cover by the fourth growing season. Determination of which individuals among the early inhabitants will successfully colonize a gap is complicated by species differences in competitive ability, thinning rates, reproductive maturity rates, and the episodic nature of opportunities for growth due to the unpredictability of disturbances (Clark 1991b). However, the early cohorts, especially those seedlings established the first year, reached a level of strong dominance by the sixth year (Peterson and Pickett 1995). All these results strongly suggest that the early stage of gap colonization is a critical period of forest regeneration.

Ultimate dominance of a gap, or which individuals will eventually replace the lost canopy trees, thus depends on many factors. Properties of the gap itself can affect future gap composition. More direct light can enter large gaps, thus giving an advantage to light-demanding species, which are typically faster growing than their shade-tolerant counterparts (Hibbs 1982; Poulson and Platt 1989). Gap orientation changes the way light enters throughout the day, causing an asymmetry in light and affecting canopy replacement patterns (Poulson and Platt 1989). The nature of the sources of colonization among species and sites, such as size of the seed bank, amount of advance regeneration, and dispersal strategy, also affect later gap composition. Poulson and Platt (1989) suggest that the chance that a species or an individual will reach the canopy of a large gap is less dependent on frequency or density of that species and more on local site conditions, what other species are present, growth rate, and physical architecture of the community.

The aforementioned properties of gaps also interact with species traits to affect species dominance. There is a broad spectrum of life history traits that both allows some tree species to capitalize on disturbances and allows for the coexistence of many species in a given community (Fox 1977). Coexistence occurs because disturbance events greatly increase the availability of regeneration niches, which provide the opportunity for a variety of species to germinate and grow (Forcier 1975). Within a gap, disturbance creates different microsites that vary in environmental characteristics, such as pits and mounds created by the uprooting of a tree in a windstorm. These microsites provide the opportunity for differential success among species depending on their particular requirements for germination and growth (Gilbert 2000; Peterson et al. 1990). Some ecologists have proposed that there are two classes of trees: pioneer species which readily colonize disturbed sites and competitively dominant climax species that will eventually regain dominance (e.g. Whitmore 1989). Although the idea of climax has been rejected by many ecologists (e.g. Pickett 1976; Sousa 1984) because it implies the possibility of an ultimate stasis in community composition, there is no doubt that species respond at different rates to disturbance.

Possibly the most important distinction among life history traits with respect to disturbance response and gap colonization is shade tolerance level. Gaps are important in forests largely because they temporarily increase the availability of resources, and of light in particular (Canham and Marks 1985). Shade intolerant species rely on gaps and the higher light levels they provide and are generally absent from the understory of undisturbed forest. However, although shade tolerant species may be capable of persisting in the understory of an undisturbed canopy, the dependence of shade tolerant species on gaps is indicated by periods of release and suppression of growth (Canham 1989). That species of varying life histories all rely on gaps for growth further illustrates the importance of natural disturbance in forest dynamics.

Studies of disturbance ecology have focused both on the importance of small scale factors, such as gap size, microsites, and damage type (e.g. Hibbs 1982; Runkle 1982; Peterson et al. 1990) and on how gap dynamics function on a landscape level (e.g. Foster 1988a; Foster 1988b). This larger scale investigation is based on the idea that one disturbance will likely create multiple gaps, and multiple disturbances may occur over the time period required for a single gap to regenerate. The result is a landscape consisting of gaps in various stages of regeneration, creating a mosaic (i.e. Clark 1991a); this conception of landscapes has led to the study of patch dynamics, which place gaps in a broader context. Both small and large-scale studies are integral if we are to obtain a complete picture of how forest regeneration occurs and what its consequences will be.

Disturbances are thus important determinants of community structure and composition, and comparisons of disturbed sites to intact sites can provide further elucidation of the particular effects of disturbance in a given community. Peterson and Pickett (1995) found that a large (400 ha) blowdown had higher species richness, total percent cover, and total seedling density than the intact forest. Species richness in gaps was shown to have a strong positive correlation with gap size (Runkle 1982). Mou and Warrillow (2000), however, found that 2 years after an ice storm, seedling density was higher in the intact forest than gaps, which they attributed to possible damage of advance regeneration, the effect of a large number of very small gaps on the data, and site conditions particular to the forest of study. This discrepancy suggests that there may be high variability in the characteristics of disturbed sites relative to intact ones, and thus we are not yet at the stage of understanding the generalized effects of gap disturbances (i.e. effects across community types).

This study examined some aspects of gap dynamics in an old-growth hemlock forest in Vermont, the Battell Research Forest (BRF). It is one of the few remaining portions of old-growth hemlock-dominated forest in Vermont and probably the northeast United States. Most studies of forest dynamics have taken place in second-growth forests (Dunn et al. 1983). It is important to conduct studies of natural disturbances in old-growth forests because many of their trees have likely survived multiple disturbances, thus, they better represent the historical and continuous nature of disturbance response. The lesser degree of anthropogenic interference also allows for more subtle detection of changes in the forest and/or region, such as changes in climate, disturbance regime, and species interactions (Foster et al. 1996).

The BRF has been subject to several types of natural disturbances. In prior centuries, the primary disturbance regime was fire on a 150-200 year return interval, but with periods when fire came at a higher frequency, the last period of which occurred between 1806/7 and 1851/2 AD (Mann et al. 1994). This may have been superimposed on a disturbance regime of wind, which according to the frequency of hemlock release events from a reconstruction study occurred every 5-50 years in the lifetimes of these trees (several hundred years) (Mann et al., unpublished). The last two large disturbances to affect the BRF were the Great Appalachian Windstorm of 1950 (Mann et al. 1994) and an ice storm that affected a large portion of the northeastern United States and southeastern Canada in January of 1998.

Ice or glaze storms are a common disturbance in the Northeast and Midwest, but they are more often destructive in the southern United States (Mou and Warrillow 2000; Oliver and Larson 1990). In ice storms, super-cooled rain can freeze on tree limbs, covering them in a thin film or with up to 20 cm of ice. In more severe cases, the added weight of ice on the limbs of a tree may cause it to snap or uproot (Oliver and Larson 1990). The trees that have fallen create gaps in the forest much like gaps created by a windstorm. Glaze storms in northern New England can occur with a frequency of two events per decade, making them among the most frequent forest disturbances (Irland 1998); however, the impact of ice storms on forest dynamics has not been well-studied, even though they probably play a fundamental role in affected forests (Hooper et al. 2001). The 1998 ice storm was very severe: nearly one million acres of forests were damaged in Vermont, of which approximately one-third was heavily damaged (meaning subsequent growth was affected) (Irland 1998). The storm brought down 7-10% of the total aboveground biomass in an old-growth hardwoods forest in Quebec, ranking it among the most damaging ice or windstorms on record for forested landscapes (Hooper et al. 2001).

In this study, I documented forest regeneration in gaps created by the 1998 ice storm in order to understand the early period of regeneration and conjecture about the future of a small old-growth forest. Mann et al. (unpublished) suggested that fire suppression in the BRF may lead to a decrease in the dominance of conifer species (pines and hemlock) and an increase in the northern hardwood species because the latter are preferentially recruited into gaps. The 1998 ice storm represented another gap-making event, and thus an opportunity to look at this hypothesis critically. A greater relative abundance of northern hardwood species to hemlocks in the gaps and relative to the intact forest may suggest that an ongoing compositional change is occurring in the BRF.

This study examined the composition and abundance of woody plants found in the understory of gaps and in intact forest sites, addressing the following questions:

(1) Did seedling stem density change in gaps from 2 to 4 growing seasons after the disturbance? If so, are there differences among species?

(2) Were there differences in composition, density, and relative abundance of species among gaps and between the gaps and the intact forest?

(3) Were the majority of individuals in the understory of a gap established before or after the 1998 ice storm?

(4) Did the quantitative presence of hemlock versus northern hardwood species differ in the gaps and/or in the intact forest, and, if so, what are the implications of these differences on the future of the forest?

Study site

This study was conducted in the Battell Research Forest (BRF), administered by Middlebury College since 1911 and located near East Middlebury, Addison County, Vermont (44°02'N, 73°05'W). The BRF is approximately 42 ha in size and elevation ranges from 180 m to 400 m on this steep western escarpment of the Green Mountains (Mann et al. 1994). The climate of Vermont is humid and continental. Moisture conditions within the BRF vary from xeric hill slopes to mesic stream gullies and spring-fed fault zones (Mann et al. 1994). Slope of the study site ranged from 12° to 44°. Soils are shallow, rocky, and disturbed by creep and slumps (Mann et al. 1994).

The BRF is dominated by hemlock (*Tsuga canadensis*), with patches of codominance with red pine (*Pinus resinosa*) and white pine (*P. strobus*) and patches with greater importance of northern hardwoods. The adjacent lands of Robert Frost Mountain are covered in a northern hardwoods forest that has been repeatedly logged in the past 200 years (Mann et al. 1994). There is no evidence of logging in the BRF and some living pines are several hundred years old (Mann et al. 1994). The BRF was protected from logging by steep slopes, fire damage, and, more recently, the wish for preservation set forth in the deed of the land by Joseph Battell to Middlebury College in the early 20th century (Mann et al. 1994).

Methods

Sampling Methods

Data collection was concentrated in September through November 2001 in 4 gaps created by the January 1998 ice storm. In this study, a gap was considered the vertical opening of the canopy created by the fallen trees and extended to the bases of the living trees along the gap's perimeter. These gaps were originally chosen for study by Gilbert (2000) immediately after the ice storm. Their origin is thus certain. Her criteria for gaps were that they be similar in size and in close proximity, i.e. less than 100 m apart, to reduce the amount of between-gap variability. The gaps ranged in size from 402 to 650 m^2 (Table 1), as determined by the equation of an ellipse ($A=\pi * length * width/4$), which is roughly the shape of a gap. All were created by multiple trees (range of 7 to 12 gapmakers). All gaps had a surrounding canopy dominated by hemlock or hemlock with a supercanopy of white pine.

At the widest point of each gap, 3 evenly spaced transects were run the length of the gap at an angle equal to the angle of the longest axis of the gap. On each transect, 1 m^2 plots were placed 10 m apart, each of which was permanently marked with a PVC pole in the SW corner. The number of individuals of each woody plant species was counted, and height of each individual and dbh of saplings were measured in each plot. Seedlings were <1.3 m in height, while saplings were ≥ 1.3 m and <2.5 cm dbh, and trees were ≥ 2.5 cm dbh. Yellow birch (*Betula lutea*) and black birch (*Betula lenta*) were lumped into one category (to be called "*Betula* spp.") due to the difficulty of distinguishing seedlings. Each seedling and sapling was permanently marked with a metal numbered poultry tag.

Gilbert (2000) selected her plots in the gaps randomly. A 50 m transect tape was placed along the northern edge of the gap. After a random distance along the transect was chosen, she traveled south across the gap for another random distance. Twenty plots per gap were chosen in this manner. Each plot sampled in 1999 was 0.25 m^2.

In order to assess the composition of the forest surrounding the gap, each tree within 3 m of the gap perimeter was identified and counted. The abundance of each species of gapmaker, the trees creating the gap, was also measured for each gap. Intact forest plots were also sampled. An intact forest plot was defined as a plot in close (within 20 m) proximity to its respective gap but located under a closed canopy (<25% of canopy open, or without the shading of trees). It was not assumed that they would be completely undisturbed by the gap-making event, but rather that they represent regeneration under a closed canopy forest. To select the areas for intact forest plots, I started at the perimeter trees at the widest and longest points of the gap and traveled 10 m in the cardinal direction moving away from the gap. If a suitable (i.e. closed canopy forest) area was not reached in these 10 m, then I traveled another 10 m in a southerly direction. Only 3 intact forest plots were sampled for each gap because there was always some other physical limitation, e.g. Abbey Brook or cliffs. Due to these limitations, the proximity of the study gaps to each other, and the large number of additional small gaps spread throughout the BRF, it was not possible to extend the intact forest plots further away from the gaps. Intact forest plots were each 25 m^2. All individuals in the intact forest plots were counted, and height and dbh (for saplings and trees) were measured. For the remainder of this study, plots will be referred to by either "gap" or "intact forest" and the corresponding number.

Statistical analysis

A fifth gap (Gap 4) was investigated but is not included in any analysis. Because Gilbert (2000) used a plot-based sampling method, although her plots were selected randomly as opposed to the systematic layout of this study, it was possible to compare the total stem and species density data of the two studies. Hereafter, these datasets will be differentiated by year of data collection (1999 or 2001). Densities and relative abundances of seedlings and saplings of each species were calculated for each plot. Only 2001 data were used in the analysis of relative abundance because no intact forest data were available for 1999. All statistical tests were performed on individual species (when sample size was sufficiently large) and on one category of species: the northern hardwoods. Northern hardwoods included all deciduous species sampled: red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), striped maple (*Acer penslyvanicum*), red oak (*Quercus rubra*), swamp oak (*Quercus bicolor*), *Betula* spp., paper birch (*Betula papyrifera*), beech (*Fagus grandifolia*), pin cherry (*Prunus pensylvanica*), *Amelanchier* spp., elm (*Ulmus americana*), mountain maple (*Acer spicatum*), and silver maple (*Acer saccharinum*).

In 1999, Gilbert (2000) had found that 5 seedling species were abundant and widespread enough to use for statistical analysis: hemlock, yellow birch, red maple, paper birch, and pin cherry. In 2001, densities were only high enough to do analyses on three species: hemlock, red maple, and *Betula* spp. In addition, paper birch and sugar maple had enough of a presence to be included in relative abundance analyses. Because it is likely that seedlings identified as yellow birch in 1999 also could have been black birch due to its prevalence in the BRF, direct comparison of 2001's *Betula* spp. data and 1999's yellow birch data will be made. Both will be referred to as *Betula* spp.

In order to compare the presence of hemlock with that of the northern hardwood species, paired t-tests were performed on the densities of these species groups. Pearson's correlations were performed to look at possible relationships between mean relative abundances of hemlock and northern hardwoods for 3 age classes: seedlings, surviving canopy trees, and fallen gapmakers.

To look at the change in density of total stems and individual species between the years the gaps were studied, mean seedling densities per gap were compared with a paired t-test. A nested analysis of variance (ANOVA) was performed on 1999 seedling densities using time of establishment (pre or post ice storm colonization) and gap as fixed factors to determine what the major seedling source was. Whether a seedling had established before or after the ice storm was determined by counting nodes, or, when this was not possible, by size class 2 growing seasons after the ice storm (Gilbert 2000). An analysis of establishment time was not done for 2001 seedlings because seedling age could not be reliably determined.

Further tests were performed to examine the amount of variation among gaps. I performed one-way ANOVAs to look at differences in total seedling and sapling densities and the densities of individual species among gaps. Total sapling density in 1999 was not analyzed with an ANOVA as few saplings were found. Only hemlock, red maple, and *Betula* spp. had high enough densities to analyze independently. To look at differences in relative abundances of individual species among gaps, Kruskal-Wallis tests were performed.

Gaps and intact forest were compared for both density and relative abundance. Paired t-tests were performed to compare mean seedling densities between gaps and associated intact forest plots. Mann-Whitney U-tests were performed using relative abundance data for each site between the gap and the intact forest for individual species and the northern hardwoods group. The tie-corrected significance values (asymptotic 2-tailed significance) of this test are reported rather than the exact significance because the former represent a more conservative form of the test especially with respect to how it ranks tied values (Dytham 1999), of which there were many in the data. All statistical tests were performed using SPSS for Windows (Release 10.0.0 [1999], Standard Version).

Results

Total seedling density

In this study (sampling year 2001), mean seedling stem density differed across gaps (F=2.853, p=0.051) (Figure 1). Gap 1 had the highest density of seedlings. The range in density for individual gap plots was 0-41 stems/m^2; stem densities of gaps were not distributed uniformly; there were several outliers with much higher densities than the other plots (Figure 2A). Over 25% of all 2001 gap plots had no seedlings: Gaps 1, 3, and 5 had 2 empty plots each, while Gap 2 had 4 empty plots. Seedling stem densities of the intact forest plots were lower than in the gaps, but this was not significant (t=-2.012, p=0.138) (Figure 1). The range of means for the intact forest plots was 0.16-2.2 stems/m^2 (Figure 2B), but when the 3 intact forest plots at each site were combined, the range of these means was smaller at 0.81-1.16 stems/m^2. The range in plot seedling densities for 1999 was large (0-75 stems/m^2), but there was a more even distribution than in 2001 with each density category represented (Figure 2C).

Seedling densities were lower 4 years after the gap-making event than 2 years afterwards (t=-4.85, p=0.017) (Figure 3). Rank abundance did not change for the gap with the highest density (Gap 1) or for that of the lowest density (Gap 2) from 1999 to 2002 (Table 2). The 2 gaps with intermediate densities did change rankings. Gaps 2 and 5 both experienced a reduction in seedling density between 1999 and 2001 of over 75%, while Gaps 1 and 3 decreased by about one-third.

There was a pattern in the percent change in density of groups of species differing in shade tolerance level. The shade intolerant species decreased 86%, the intermediate species 75%, and the tolerant species 28% (Figure 4). The average change in density was –70% for all 5 of the species included in these groups combined.

Total sapling density

Few saplings were found in any gap. In 1999, saplings were only found in Gap 5, but in 2001, they were present in every gap except Gap 2 (Figure 5). Overall, there was an increase in the number of saplings from 2 years to 4 years after the gaps were formed (from 3 to 16 saplings total). However, there was a decrease in the density of saplings found in Gap 5 from 1999 to 2001. Mean sapling density in gaps was not significantly different between years (t=-0.712, p=0.528). There was a difference in sapling density among gaps as sampled in 2001 (F=4.985, p=0.006). Sapling density in that year was significantly higher in Gap 3 than Gap 1 (p=0.024) and Gap 5 (p=0.007). Because so few saplings were found in 1999, no statistical test was used to compare gaps. There was no difference in sapling density between gap and intact forest in 2001 (t=0.983, p=0.398). Sapling density between sites in the intact forest seemed to vary less among sites than in the gaps.

Composition

Twenty species were found in the BRF in 2001 (Table 3). Of these species, 10 were found as seedlings or saplings in gaps in 2001, and 11 were found in gaps in 1999. In 2001, species richness was higher in the intact forest than the gap for all 4 sites (Table 4). The species found as seedlings in the 2 sampling years differ slightly. Mountain maple and silver maple were found only in 1999, and black birch was found only in 2001.

In 2001, five species were found as seedlings in the intact forest that were not found in the gaps: mountain maple, silver maple, swamp oak, elm, and *Amelanchier* spp. (an unidentified juneberry).

Many fewer species were found as saplings than seedlings in both the intact forest and the gaps. Of the 3 saplings found in 1999, 2 were striped maple and 1 was red maple. In 2001, the majority of saplings found in gaps were *Betula* spp., by almost an order of magnitude (Figure 6). Striped maple, sugar maple, and pin cherry were also present. In the intact forest, most saplings were striped maple, with smaller amounts of red maple, sugar maple, mountain maple, *Betula* spp., and hemlock. More species were represented by saplings in the intact forest, and pin cherry was the only sapling species occurring in the gaps but not the intact forest.

Of the canopy trees around the perimeter of the gap, hemlock was more than 10 times more abundant than any other species (Figure 7A). The minor gap perimeter species were, in order of decreasing total abundance: black birch, red maple, yellow birch, paper birch, white pine, beech, and red spruce (*Picea rubens*). Gaps 2 and 5 showed a greater importance of white pine in the supercanopy, which may have been co-dominant with hemlock in these adjacent gaps. Trees sampled in the intact forest were mostly hemlock, with a few individuals of rare species. The gaps were created by 7-12 gapmakers each, most of which were hemlock, but also included, in decreasing order, paper birch, black birch, red maple, white pine, and red pine (Figure 7B).

Red maple

Red maple was the most variable in distribution of all the abundant species. There was no difference in mean density of seedlings established before or after the 1998 ice storm (F=0.105, p=0.981) (Figure 8A). However, red maple far surpassed other species with the highest density of seedlings established before the 1998 ice storm, as measured in 1999, followed by *Betula* spp. and hemlock with very small densities (Figure 9). There was a significant difference in red maple seedling density among gaps in 1999 (F=14.305, p=0.000) and in 2001 (F=3.722, p=0.020) (Figure 8B). There was no significant difference in red maple density between gaps and intact forest (t=0.979, p=0.400). In 2001, red maple was only found in Gaps 1 and 3, being almost entirely concentrated in Gap 1, whereas it was found in all intact forest plots. Density of red maple was higher in Gap 1 than all other gaps in both 1999 (Gap 2 p=0.000, Gap 3 p=0.000, Gap 5 p=0.002) and 2001 (Gap 2 p=0.035, Gap 3 p=0.041, Gap 5 p=0.057). Out of all gap plots, that with the highest density (41 stems/m^2) was almost all red maple.

There was a significant difference in the mean relative abundance of red maple among gaps (H=13.652, p=0.003) (Figure 10). Gap 2 showed a significant difference in the mean relative abundance between the gap itself and the associated intact forest area (U=5.50, p=0.005); all other gaps were not significant.

Betula spp.

For the 1999 data, there was a significant difference in *Betula* spp. (yellow and black birch) density between the two establishment times (F=2.592, p=0.039), with more individuals establishing after the ice storm (Figure 10A). *Betula* spp. were the most evenly distributed species in 2001; they were found in all gaps in both 1999 and 2001 and in all intact forest sites. As such, there was no difference in *Betula* spp. seedling density among gaps in 1999 (F=0.185, p=0.906) or in 2001 (F=0.308, p=0.819) (Figure 11B). Density was significantly lower in the intact forest than gaps (t=3.865, p=0.031) (Figure 11B). There were no significant differences in relative abundance of *Betula* spp. among gaps (H=1.190, p=0.755) or between gaps and intact forest at any site (Figure 12).

Sugar maple

Sugar maple showed high variation in presence or absence among gaps and between gaps and intact forest areas (Figure 13). There was a significant difference in its relative abundance among gaps (H=11.103, p=0.011). Sugar maple was not found at Site 5 in either the gap or intact forest. At Site 2, it was only found in the intact forest. Site 2 was the only site for which the gap-intact forest comparison of relative abundance was significant (U=5.500, p=0.005).

Paper birch and pin cherry

Like sugar maple, paper birch showed high variation in presence or absence. It was found at all sites, but at Site 1 only in the gap and at Site 5 only in the intact forest (Figure 14). Relative abundance did not differ significantly among gaps (H=1.190, p=0.755). The only site with a significant difference in relative abundance between the gaps and the intact forest was Site 5 (U=4.00, p=0.015).

Paper birch and pin cherry seedling density decreased from 1999 to 2001 to the extent that their densities no longer provided a sufficient sample size to be analyzed. This decrease was significant for pin cherry (t=3.584, p=0.037), but not for paper birch (t=1.484, p=0.235).

Hemlock

In 1999 hemlock seedlings that had established before the ice storm were only found in Gaps 1 and 3 but there was no significant difference in the densities by establishment time and gap (F=1.578, p=0.183) (Figure 15A). In 2001, hemlock density in the intact forest plots was lower than in gaps (t=2.626, p=0.079), and the range of densities between sites was smaller (Table 5) (Figure 15B). There were no significant differences in hemlock density among gaps in 1999 (F=1.897, p=0.148) or 2001 (F=0.406, p=0.749). Hemlock seedlings were found in all gaps and intact forest sites in both 2001 and 1999. Gap 3 appeared to be an anomaly in the data as it was the only time measured density was higher in 2001 than in 1999, for any species, perhaps suggesting further recruitment of seedlings between the sampling periods or sampling variation.

Mean relative abundance of hemlock seedlings differed significantly among gaps (H=8.392, p=0.039) (Figure 16). Hemlock relative abundance in the seedling community was high in Gaps 3 and 5 while much reduced (nearly 4 times less abundant) in Gaps 1 and 2. The lowest values of relative abundance for both gap and intact forest were found in Site 2. Relative abundance did not differ significantly between intact forest and gap at any site.

Northern hardwood species

Post 1998 ice storm establishment accounted for a greater proportion of northern hardwood species seedling density than pre ice storm establishment, particularly in Gaps 2, 3, and 5 (Figure 17A). This difference was marginally significant (F=2.176, p=0.074). The mean seedling density of all northern hardwood species, analyzed together, was different among gaps in 1999 (F=3.586, p=0.023) and in 2001 (F=3.745, p=0.013) (Figure 17B). There was no significant difference in density between the 2 sampling years by a nested ANOVA, but the trend shows a large decrease in density from 1999 to 2001 (F=1.778, p=0.138). Northern hardwood seedling densities in Gap 1 were much higher than any other gap for both years and for both pre or post establishment groups. There were no significant differences in the density between gaps and intact forest (t=1.345, p=0.271). With the exception of Gap 1, in 2001 seedling densities in the gap and intact forest at each site were similar.

The relative abundance of northern hardwood species was greater in the intact forest areas than the gaps, but this trend was not significant at any site (Figure 18). The differences in relative abundance among gaps were not significant (H=3.573, p=0.311).

Hemlock vs. northern hardwood species

Hemlock seedling density in gaps was significantly lower than that of northern hardwoods in 1999 (t=-3.935, p=0.029) (Figure 19A) but not in 2001 (t=-1.078, p=0.360) (Figure 19B). In 1999, northern hardwood densities were much higher than hemlock in gaps, but the difference between the 2 narrowed by 2001, with the exception of Gap 1. Mean percent change in density between 1999 and 2001 was higher for northern hardwoods at –68% than hemlock at –28%. Densities of hemlock and northern hardwoods differed in the intact forest in 2001(t=-3.768, p=0.033); northern hardwoods had much higher densities than hemlock (Figure 19C).

A comparison of the relative abundance of hemlock and northern hardwoods shows that hemlock has a slightly greater relative abundance in 2 of the gaps (Gaps 3 and 5) while northern hardwoods have a much greater importance in Gaps 1 and 2 (Figure 20A). In the intact forest areas, however, northern hardwoods have a higher relative abundance than hemlocks at all sites; the difference is most pronounced at site 2 (Figure 20B). There were almost 7 times more saplings of northern hardwood species in gaps than hemlock.

No correlations were found between the relative abundances of hemlocks and grouped northern hardwood species between seedlings, trees, and gapmakers.

Discussion

The early cohort: establishment, density, and mortality

The early cohort of trees establishing after a canopy disturbance appear to be important in the forest regeneration process. Gaps in the canopy of a forest create patches with different environmental conditions than areas of the forest with a mostly closed canopy (intact forest). Typically, the removal of the canopy provides the plants growing in gaps with greater resource availability and creates different microsites for establishment (Peterson and Pickett 1995). Individuals colonizing a gap may come from the seed bank, newly dispersed seeds, and/or advance regeneration (Canham and Marks 1985). The majority of the individuals comprising the early cohort in the BRF gaps established after the 1998 ice storm. This finding suggests that in the BRF the seed bank and/or seed dispersal are the most important sources for forest regeneration in gaps. This finding is surprising in part because some of the species of the BRF, especially hemlock, are known to rely heavily on advance regeneration (Godman and Lancaster 1990). The fact that hemlock is currently the dominant species of the BRF then makes its lack of advance regeneration even more important.

Runkle (1982) found that larger gaps tended to have lower sapling densities, which he attributed to damage and ground coverage by debris. Because each gap in the BRF was created by multiple gapmakers, there is a considerable amount of debris within the gaps, so Runkle's hypothesis may also explain the lack of advance regeneration in the BRF. However, there were small densities of seedlings and saplings found in the intact forest, which represent advance regeneration. Densities of pre ice storm established seedlings in the gaps were between 2-6 times higher than the densities of seedlings in the intact forest, however, this difference is not as great if one excludes the large quantity of red maple seedlings in Gap 1. The density of saplings in the intact forest is about an order of magnitude lower than the density of seedlings there. Saplings were present in all intact forest sites in 2001, but only in 1 gap in 1999 and 3 gaps in 2001, so the data may provide some support for Runkle's hypothesis that advance regeneration is being damaged by the disturbance. A similarly surprising finding with respect to saplings, however, is that there was no difference in sapling density between the gaps and the intact forest. This suggests that even with the high resource environment of the gaps, seedling are not growing into the sapling age class (≥1.3 m) within the first four years after disturbance. Finding only a small amount of advance regeneration in the BRF is surprising, especially when coupled with both a dominant species that tends to rely on advanced regeneration and a surprising lack of growth by seedlings into the sapling age class by the fourth growing season.

In the gaps in the BRF created by the 1998 ice storm, seedling densities, which were very high 2 growing seasons after the event (1999), decreased significantly by 4 growing seasons after the disturbance (2001). Three explanations exist for this pattern: (1) sampling variation, (2) growth into another age class, and (3) mortality. Although methodology differed between the 2 years of data collection, there was nothing about sampling that should lead to a systematic bias in the data. Thus sampling variation is an unlikely explanation.

The second potential explanation for the decrease in density from 1999 to 2001 is that in those two years, some seedlings could have grown enough to be saplings in 2001 and thus be excluded from analysis. I have already shown that there are few saplings in the gaps. The total number of saplings found increased from 3 in 1999 to 16 in 2001. However, this was in comparison to 182 seedlings found in 2001, suggesting that sapling have only a relatively small contribution to the understory of the gaps. If growth of seedlings into the sapling age class were the explanation for decreased seedling density, overall (seedling and sapling) stem density should have remained relatively constant from 1999 to 2001. In fact, overall stem density also declined sharply between the 2 sampling years (Figure 20). Although growth into another age class may account for a small amount of the density difference between years, the difference in seedling density is large enough that this explanation cannot account for much of it.

Mortality is thus the most likely explanation for declining seedling density. The decrease in seedling density documented by the fourth year after the ice storm is supported by previous studies. Soon after a disturbance, resources will again change as gaps are colonized and individuals begin using these resources. Seedling establishment is typically limited to a brief period after disturbance (Canham and Marks 1985; Peterson and Pickett 1995) because space and other resources are limiting and/or transient (Canham and Marks 1985). Density thus tends to decrease after the first few years following gap formation (Peterson et al. 1990) because the plants that have colonized the gaps proceed to compete for these limiting resources, and competition-related mortality is high.

Oliver and Larson (1990) have characterized the forest regeneration process following disturbance into 4 stages. The first stage is the stand initiation stage, which is when establishment occurs. In the second, the stem exclusion stage, mortality and growth of surviving individuals occurs. The timing of the change from the stand initiation stage to the stem exclusion stage varies greatly among forest types. The third stage is the understory reinitiation stage, in which an understory of non-woody plants and shrubs as well as advance regeneration reappears. Finally, the old-growth stage shows natural death of canopy trees and the growth of understory trees into the canopy.

The decline in density observed in seedlings in the BRF suggests that the 1998 ice storm gaps have rapidly moved from the stand initiation stage to the stem exclusion stage. However, there is not much indication in the literature of how and when this process occurs because few studies exist of the growth and mortality of seedlings and saplings. Most studies including data on change in density resulting from disturbance are on a larger spatial scale than the medium sized gaps of the BRF (i.e. Dunn et al. 1983; Foster 1988a; Peterson and Pickett 1995; Whitney 1984). Theoretically, as explained in a model by Clark (1991b), density should decrease by several orders of magnitude from the time of colonization until reproductive maturity. Foster (1988a) reconstructed the history of the Pisgah Forest in New Hampshire after it was severely affected by the 1938 hurricane on a forest-wide scale. He found that density increased by 14 orders of magnitude from before 1938 to 4 years later. Around 40 years later, it had decreased by a magnitude of 5. Because the stems in the 1998 ice storm gaps are still at the understory level, conversion from the stem exclusion phase to the understory reinitiation stage will not likely happen for at least a couple decades in the BRF. Thus, the present composition of the ice storm gaps can be expected to change in the next couple decades of the stem exclusion stage, assuming that species-specific mortality will occur.

Seedling densities in the 4 ice storm gaps varied widely in both 1999 and 2001, which supports previous findings of wide variance of colonizing population densities among disturbed areas (Connell 1989). Peterson and Pickett (1995) found that mortality was greatest in plots with very low or very high densities. In the BRF, the 2 gaps experiencing the greatest declines in density were those ranked fourth (Gap 2) and second (Gap 5) in 1999. Density in these gaps declined about twice as sharply as in Gaps 1 and 3. High mortality in a high-density gap would be explained largely by competition for resources, and this may not have occurred to its full extent by the fourth growing season. In a low-density gap, high mortality could be due to poor site conditions for establishment and growth and/or a shortage of colonizing sources. Since only 4 gaps were examined, it is difficult to make judgments based on rankings of either density or apparent mortality rates as shown by declines in density, so any combination of the above factors could have played a role in seedling mortality in the BRF gaps.

Species differences in the colonization of gaps

In 1999, the majority of seedlings of most species established after the 1998 ice storm. The only exception was red maple, which had a higher density of pre-ice storm than post-ice storm established seedlings in Gap 1 and near equal amounts in Gap 5. *Betula* spp. and hemlock both showed very little pre-ice storm establishment. Although the northern hardwood species as a group showed considerable pre-ice storm establishment, this was most likely a result of high numbers of red maple.

Species differ in their life history characteristics, and these differences may permit the coexistence of species at any given point in time. The interrelationship of species is important to forest composition, species' survival, and the provision to the forest of a mechanism for recovery from disturbance (Forcier 1975). Thus, there are certain patterns of revegetation that forests seem to follow when disturbed and/or when gaps are formed. For example, gaps are usually dominated first by shade intolerant species, which tend to be fast growing, but as these species usually have a trade-off in higher mortality rates and reduced longevity, the shade tolerant, slow-growing species eventually achieve dominance (Foster 1988a). Thus, we would expect to see greater representation of the shade intolerant and intermediately tolerant species classes in the high-light environment of gaps because that is where they are able to best compete. Because the supply of light, space, and other resources decreases within several years of the disturbance event, density of these species should also decrease. We would thus expect to see high mortality of seedlings of the shade intolerant species at this point, except for those individuals that are able to maintain a position in the light above the rest of the cohort. In gaps where densities of species declined between 1999 and 2001, I can therefore interpret the declines in density as an index of mortality. Mortality rate, quantified as mean percent change in density between years, was expected to be highest in shade intolerant species, followed by intermediately tolerant species, then tolerant species.

Of the portion of the BRF studied, among the species widespread enough in both years to allow comparison, the shade intolerant species include paper birch (Safford et al. 1990) and pin cherry (Wendel 1990). Species of intermediate shade tolerance include black birch (Lamson 1990) and yellow birch (Erdmann 1990) combined here as *Betula* spp., and red maple (Walters and Yawney 1990). The only shade tolerant species abundant enough for analysis was hemlock (Godman and Lancaster 1990), although sugar maple (Godman et al. 1990) and beech (Tubbs and Houston 1990) are also tolerant.

The change in density of groups of species differing in shade tolerance did follow the predicted pattern. The shade intolerant species decreased the most, followed by the intermediately tolerant species, which were then followed by the shade tolerant species. Because each tolerance group was composed of very few species (between 1 and 3), some of this pattern may be an artifact. However, the pattern is so clear that it strongly suggests that different tolerance groups have different mortality rates within gaps.

Neither shade intolerant species was found in very high densities even in 1999, perhaps because they are less important species in the hemlock-dominated community of the BRF. However, paper birch and pin cherry were 2 species for which density declines were large, and by 2001, few seedlings were found. Both species decreased by 85-86% between the 2 years. Growth into another age class cannot explain much of this density difference as only 2 pin cherry saplings were found in gaps in 2001, not enough to explain its decline in the seedling class. It was surprising that no paper birch saplings were found in gaps. This suggests that shade intolerant species did initially capitalize on the high light environment, but then experienced high mortality between the sampling years.

As expected, intermediately shade tolerant species experienced less mortality than the intolerant but more than the tolerant species. Red maple and *Betula* spp. were very well represented in density in 1999, relative to hemlock, but they also declined in density by 2001 more than hemlock. Contributing to the smaller decrease in seedling density of hemlock was the unusual increase in density for the species in Gap 3 (by 62%).

However, the advantages of shade tolerance that allow hemlock to grow well (albeit slowly) in shaded conditions and support advance regeneration also permit it to germinate and establish in the same shaded conditions. Therefore, hemlock should be the most likely species to continue to establish after the gaps overall have passed from the stand initiation stage to the stem exclusion stage. In a 30-year study on dynamics in a hemlock-hardwoods forest in Michigan, Woods (2000a) found that density decreased the most among smaller trees of northern hardwood species, while hemlock was the only species for which recruitment rate exceeded mortality.

In terms of spatial patterns among gaps, hemlock and *Betula* spp. showed the most even distributions. In contrast, red maple, sugar maple, and paper birch were quite variable in distribution. All other species found in the gaps were rare. These species-specific patterns were supported in the literature. In a New Hampshire forest, Forcier (1975) found that yellow birch, relative to two slow-growing species (beech and sugar maple) was the most opportunistic, most widespread, and that it capitalized on disturbed sites for establishment. Hemlock and yellow birch have been found in close association throughout the northeastern U.S. (Woods 2000b), which has been attributed to nearly identical temperature requirements for germination (Godman and Lancaster 1990). Throughout the BRF, as well, hemlock and *Betula* spp. were found in association with each other.

Seed rain and dispersal also seem to play a large role in where species are present and in what amounts. Larger seeded species, such as red maple and sugar maple, have heterogeneous seed rain distributions, while smaller seeded species, such as hemlock and the birch species, have wider and more homogeneous distributions (Catovsky and Bazzaz

2000), consistent with what I found in the BRF. Additionally, different species tend to establish in different microsite conditions. In the Battell Research Forest itself, Gilbert (2000) found that hemlock and yellow birch seemed to specialize in microhabitats under fallen trees and in the mounds and pits of uprooted trees. Black birch seems to especially favor mounds and stony outcrops (Henry and Swan 1974). Red maple seems to have greater establishment in pits, to often reproduce via root sprouts (Henry and Swan 1974), and to often have a high dominance in large gaps, perhaps due to sprouting as a response to damage of red maples in the canopy (Mou and Warrillow 2000). The differences among species and in patterns of colonization of the 1998 ice storm gaps thus seems to depend on a combination of unique life history traits.

Differences between gaps and the intact forest

Because of the greater availability of resources in a gap environment, higher seedling densities would be expected in gaps than under a closed canopy. In a greenhouse study growing seeds from the seed bank under different conditions, it was found that those cohorts growing in a low light environment mimicking the canopy experienced high seedling mortality leading to communities of very low densities (Catovsky and Bazzaz 2000). In the BRF, seedling density in 1998 ice storm gaps was much greater than that in intact forest plots, but differences were not significant. This may be due to the high amount of variation among gaps. It may also be due to the proximity of intact forest plots to the gaps, which thus could also be exposed to more sunlight than under a canopy without any impacts of recent disturbance. However, a study of ice storm gaps conducted 2 years after their formation found seedling density to be lower in the gaps than the non-gap areas sampled (Mou and Warrillow 2000). The authors largely discounted this finding, proposing that it may have been too soon after damage for establishment to take effect, the small size of gaps may have decreased the environmental differences between gaps and non-gaps, and/or the storm could have damaged pre-existing understory communities. Very few studies have compared gaps to intact forest areas in close proximity, and the mixed results of those that have suggests that this is an aspect of gap dynamics that needs further study.

Species differed in presence/absence between the gaps and the intact forest. Twice the number of species were found in the intact forest (including perimeter trees of the gaps) than in the 1998 ice storm gaps themselves. This was expected for two reasons: (1) because the area sampled in the intact forest was larger than the gap area sampled by an order of magnitude, it would necessarily include more rare species that would be missed in a smaller sampling area; and (2) not all species would be expected to colonize a newly formed gap. For example, one single tree of American basswood (*Tilia americana*) was found in an intact forest plot. Basswood tends to germinate poorly in any conditions, but establishment is aided by a shaded environment (Crow 1990). Thus, one would not expect to find basswood seedlings colonizing a gap in the BRF. Similarly, striped maple was the most abundant sapling species in the intact forest, whereas very few striped maple individuals were found in gaps. This finding corresponds with the life history of striped maple because it grows best in shaded environments and is a common understory component of mixed forests (Gabriel and Walters 1990).

Hemlock regeneration and the future of the forest

The BRF canopy is composed primarily of hemlock but hardwood communities surround and intermingle with the small, uncut forest. Mann et al. (unpublished) found that northern hardwood species were differentially replacing fallen hemlocks in gaps created in hemlock and hemlock-pine dominated stands of the BRF by the Great Appalachian Windstorm of 1950. This was determined by locating the 1950 gaps and determining which species were dominant at that point (40 years after the disturbance). Encroachment of hardwood species may interfere with successful hemlock establishment, as has been shown in thinned hemlock stands (Lancaster 1985). What this seems to indicate is that there are two types of forest that could dominate in the BRF: the current hemlock dominated forest or a northern hardwoods forest. The early stages of hemlock regeneration in 1998 ice storm gaps may give insight on the future of the forest, especially with respect to hemlock's capacity to maintain dominance in the BRF. Four years after the 1998 ice storm, my results seem to indicate that the success of hemlock regeneration differs among sites. Compared to the northern hardwoods, hemlock had a slightly higher relative abundance in 2 of the gaps (Gaps 3 and 5) while in Gaps 1 and 2 it was much lower. Thus, if hemlock and northern hardwoods maintain their relative abundances in each gap from this point onward, they are more or less equally likely to become the dominant presence in 2 of the gaps, while it appears that hardwoods will dominate or at least have a high importance in the other 2 gaps. However, it has already been demonstrated that the 2 groups have differential growth rates and differential mortality rates. Growth rates would seem to favor the northern hardwoods, while mortality rates would seem to favor hemlock.

Especially for the 5 largest gaps in the BRF created by the windstorm in 1950, Mann et al. (unpublished) proposed that chance probably played an important role in determining which species captured these gaps. The high variability in my data is consistent with an important role for chance events in the colonization of and survivorship in the 1998 ice storm gaps as well.

However, Mann et al. (unpublished) also noted a lack of hemlock advance regeneration in some stands of the BRF. As hemlock is very shade tolerant, an understory layer of hemlock can grow underneath the canopy as advanced regeneration (Godman and Lancaster 1990), indeed, this is hemlock's main regeneration strategy. Hemlock also changes site conditions in such a way (i.e. promoting low resource conditions) to favor the recruitment of its own seedlings; thus, positive feedback may occur in hemlock stands (Catovsky and Bazzaz 2000). In New Hampshire, after the 1938 hurricane, most hemlock trees had established via advance regeneration, while seedlings that established after the disturbance were quickly overtopped by faster-growing hardwood species (Foster 1988a). Similarly, Mann et al. (unpublished) suggested that hemlock did indeed succeed as a competitor and replace itself in patches of the BRF where there was advance regeneration.

In the 4 1998 ice storm gaps, there is also an absence of hemlock advance regeneration. In these gaps, the majority of the seedlings established before 1998 and surviving in 1999 were northern hardwoods rather than hemlocks, for which pre-ice storm establishment was only seen in small densities in 2 gaps (Gaps 3 and 5). Therefore, a similar capture of gaps by hardwoods could occur in the 1998 gaps as the 1950 gaps due to a continued lack of advance regeneration. Further striking evidence for this pattern is that the seedling communities of the intact forest were composed of more northern hardwoods than hemlock, showing a possible shortage of hemlock advance regeneration under the extant canopy as well. Interestingly, a study of treefall gaps also found hemlock only as very small seedlings, even though it was prevalent in the pre-disturbance canopy (Peterson et al. 1990). Low densities of hemlock seedlings and saplings have been seen as a cause of alarm in other forests as well, with the same prediction that dominance may shift towards hardwoods (Davis et al. 1998).

However, several caveats must be made with respect to the validity of projecting the present state of forest regeneration of the 1998 ice storm gaps towards future forest composition. First, red maple, which is the source of the greatest disparity between densities and relative abundances of hemlock and northern hardwoods, is an unusual case. Previous studies have found that red maple has a high dominance in large gaps (Mou and Warrillow 2000); however, because the species sprouts prolifically but has a low long-term establishment rate (Walters and Yawney 1990), its high seedling density does not indicate it will be a dominant force in the forest. However, Abrams (1998) suggests that red maple has become more and more dominant across the New England landscape in the twentieth century due to its ability to act as both an early and a late successional species. Second, this study looks at only a brief period of time. The seedling communities of the 1998 ice storm gaps could continue to experience species-specific mortality. A comparison of two early years (1999 and 2001) showed that mortality affected northern hardwood species, which were heavily dominated by red maple, more than hemlock, so if mortality continued in this fashion, hardwoods would become increasingly less important in these communities.

Another problem with basing projections on a short-term study is its inability to pick up successional processes. In the most typical successional model, after a disturbance, the fast-growing species dominate the first generation, but they are short-lived, and are succeeded by slow-growing species with greater longevities, which will dominate until the next disturbance. In the BRF, hardwoods may represent the first generation and hemlock the second. In gaps, hemlock grows more slowly than the hardwood species (Hibbs 1982), but its survivorship is not influenced by its size (Peterson and Pickett 1995). Thus, although hemlock may not be the strongest competitor in a given situation, it may grow in the shade of the hardwoods and survive a series of suppressions and releases (as evidenced by tree ring data) in response to episodic disturbances (Hibbs 1982). Henry and Swan (1974) found that hemlock was the only species (in a forest compositionally quite similar to the BRF) that showed both releases and suppressions. In the BRF itself, most canopy hemlocks survive 2 gap-making events before reaching the canopy, suggested by the number of releases found in tree rings (BI323, spring 2002, unpublished data). In this way, even where hardwoods are dominant in early regenerational communities, hemlock may eventually reach the canopy. Runkle (1985) stressed the importance of multiple gap episodes in the lifetime of one tree for forest regeneration and species evolution. Therefore, even if data from the early stages of forest regeneration in 1998 ice storm gaps seem to suggest that hardwoods will increase in importance in the BRF, it may come to pass that hemlocks do eventually regain the canopy. Forest regeneration in gaps following disturbances takes place on a time scale of generations of trees, and a study such as this one cannot encompass a scale that large.

However, one aspect of forest composition that does clearly seem to be changing is the dominance of pines in the BRF. After the Great Appalachian Windstorm of 1950, gaps in the in the pine-dominated portions of the BRF tended to be captured by hemlocks, while, as previously discussed, gaps in hemlock-pine co-dominant portions were differentially captured by hardwoods (Mann et al. unpublished). Historically, recruitment of trees in the BRF has been conditioned by fire (Mann et al. 1994). Red pine as well as white pine is common in some patches of the forest. However, red pine has very specific reproduction and germination requirements, which are produced naturally only by fire (Rudolf 1990). White pine, on the other hand, can establish in a variety of conditions, including post-fire and post-blowdown, but it fares poorly when competing with hardwood species, especially at the seedling stage (Wendel and Smith 1990). Henry and Swan (1974) found that white pine in New Hampshire's Pisgah Forest, which had previously been characterized by a fire disturbance regime, disappeared after the 1938 hurricane because it was highly susceptible to damage (due to its location in the supercanopy) and failed to regenerate after 1938. Thus, red pine will, in the absence of fire, disappear from the BRF. Meanwhile, white pine, which is not capturing 1950 gaps nor does it show significant regeneration in 1998 gaps, may also be declining in abundance and relative dominance in the BRF.

Variability

One of the most prominent results from this study of the effect of gaps created by the 1998 ice storm on regeneration in an old-growth hemlock-dominated forest in Vermont is the amount of variability between gaps. Significant variability was found among gaps for many measures in both years. Stem densities varied among gaps, as did seedling densities and the relative abundances of several species.

The gaps were selected to be in the same forest stand, similarly sized, and in close proximity to one another (within 100m of another gap) in order to minimize the effect of environmental variables on the forest regeneration processes being studied. However, as seen by the differing relative importance of species, in both relative abundance and density, among gaps, it is evident that a great deal of fine-scale spatial variability is inherent in this system.

Part of this spatial variability may be due to how differences in site characteristics (i.e. microsites) allow for multiple, coexisting regeneration niches, thus facilitating the maintenance of species diversity (Peterson et al. 1990). Other sources of variability, such as chance, dispersal patterns, and historical contingency, are also important in forest regeneration and gap capture events. Thus, models trying to determine gap capture based on only a few parameters are largely inaccurate in determining future forest composition (White et al. 1985). Gap-creating disturbances are very important in New England forests, having a greater impact on the vegetation than any other factor, which must then constantly readjust to further damage (Foster 1988a). Thus, gap-creating disturbances are a large factor determining forest composition and forest recovery. This may be increasingly the case in the BRF in which gap-creating disturbances appear to have become the principal disturbance regime.

Mosaics characterize both intracommunity patterns, such as the site variability previously discussed, and intercommunity successional patterns that are greatly affected by disturbance (Whittaker and Levin 1977). The idea of a landscape as a mosaic composed of independent but interacting patches has been proposed and supported in many studies of gap and/or forest stand dynamics (Clark 1991a; Clark 1991b). Thus, variability within the BRF is necessarily important for the forest's development and dynamics just as variability on the larger landscape scale is an important ecological factor. A patch is a discrete area comprised of individuals similarly affected by site conditions or affected and/or recruited by a particular disturbance event. White and Pickett (1985) proposed the term "patch dynamics" to describe the mosaic because they believed that it: (1) implied a relatively discrete spatial pattern, but without putting many constraints on its nature; (2) implied the interrelationship of one patch to another and to the intact area; and (3) emphasized the capacity of the patches to change. In order to be a part of a mosaic landscape, a patch must be of a size where it begins to act as an independent stand; otherwise all parts of the patch are overly affected by the surrounding environment (Oliver and Larson 1990). The idea of patch dynamics has not only been applied to the study of gaps, but also to intact forest stands showing a high degree of heterogeneity (Davis et al. 1998; Frelich et al. 1993).

Ecologists found overriding evidence of patch dynamics within forested ecosystems. Patches seem to evolve through the interactions of many different mechanisms. Some of the environmental, ecological, and biological factors resulting in the existence of patches are local biotic and abiotic factors (White and Pickett 1985), differential life history traits of different species, such as reproductive strategies (Forcier 1975) and dispersal (Peterson et al. 1990), effects of species on the surrounding environmental conditions (Catovsky and Bazzaz 2000), competitive interactions (Frelich et al. 1993), microsite differences (Peterson et al. 1990; Webb 1988), natural disturbance history (Foster 1988b), land use history (Foster et al. 1998), and chance (Clark 1996). The variability among patches is very important in gap-creating disturbances, if the gaps are large enough to be considered patches, because that variability has a large impact on overall forest composition.

The idea of patch dynamics highlights several important features of the BRF. First, the hemlock-dominated BRF may be compositionally different from the second or third growth hardwood forests that surround it on Robert Frost Mountain, but it is not isolated from them; they are part of the same landscape and thus are subject to similar factors as well as have influence on each other. For example, surrounding hardwood forests may contribute substantially to seed rain in the BRF and thus influence the composition of gaps. A complete understanding of the interaction between hemlocks and hardwoods in the BRF requires consideration with respect to how the BRF, as a patch, interacts with the surrounding hardwood-dominated landscape. Secondly, different patches comprise the BRF. In some of these, hemlock is not dominant; in others, a lack of hemlock regeneration suggests that hemlock may not maintain its dominance (Mann et al., unpublished). Forests of a small absolute area (like the BRF) are not likely to be in equilibrium (Sousa 1984). Thus, the interactions between the patches within the BRF may also be important determinants of the future composition of the forest.

A role for exogenic factors: disturbance regime and anthropogenic interference

Regeneration is not isolated from exogenic or endogenic aspects of forest dynamics. A forest gap, if it were placed in isolation, probably would show succession from fast to slow growing species over the course of two or more generations, and then be maintained in a steady-state forest composition until the trees died and the cycle began anew. However, support for the idea of the existence of a steady state forest has diminished in favor of emphasizing variability and the role of disturbance as the major force provoking compositional change (Foster 1988a; Henry and Swan 1974). Different kinds of disturbances favor different suites of species (Foster 1988b; Runkle 1985).

There is strong evidence that the BRF is dominated by superimposed disturbance regimes of fire and wind (Mann et al. 1994). The last interval of fire frequency was 1800-1850, while the last windstorm up until the ice storm of 1998 (which created windstorm-like gaps) was 1950 (Mann et al. 1994). In the BRF, fires have resulted in the preferential recruitment of conifers (especially pines) (Mann et al. 1994), while windstorms favor a shift towards increasing dominance of hardwood species (Mann et al., unpublished). There exists the possibility that fire already has or will become a less frequent force in the BRF due to fire suppression and a change in the composition of the forest surrounding the BRF due to land use history in the past century. The small size of the BRF could also play a role, as it could place the scale of the disturbance mosaic at odds with the scale of forest. For example, fires may be less likely in a small stand because they may stop at stand boundaries, due to related changes in soil or topography (Hemstrom 1979). Fire suppression could lead to a replacement of the fire-recruited species to the species successful in gaps due to the associated change in regeneration niches available (Clark 1991b). This hypothetical fire suppression would result in a change of disturbance regime for the BRF. A forest may respond to a new disturbance regime in a novel fashion, especially with respect to the temporal qualities of the disturbance (Clark 1996).

Hemlock is recruited by both fire (Henry and Swan 1974; Mann et al. 1994) and windthrows (Godman and Lancaster 1990; Mann et al. 1994). The establishment of hemlock seedlings requires neither of these disturbances (Frelich et al. 1993), although reaching the canopy may indeed depend on disturbance. As such, the maintenance of hemlock domination itself is not threatened by a gap-creating disturbance, and in fact may be favored given that there is advance regeneration in the forest. This does not seem to be the case in the BRF. In the case of the 1998 ice storm, although half of the gaps in the BRF showed early cohort dominance by hemlock, it is too early to determine the future importance of hemlock in these gaps. It appears, nevertheless, that even if northern hardwoods have increased in importance in the last century, hemlock dominance in the BRF is not immediately threatened.

However, several factors could interact to decrease the importance of hemlock in the BRF. First, an increased return interval of windstorm-like disturbances would continue to recruit hardwood species and maintain the patches at an early successional state, thus hemlock would remain suppressed. This proposal may not be far-fetched as the 1998 ice storm was attributed to an El Niño effect (Helvarg 1998), which causes the moderation of winter temperatures, which in turn may become more and more important in a world affected by global warming. Hemlock is disproportionately susceptible to windstorm damage (Foster 1988b; Godman and Lancaster 1990), thus the stands and/or patches of hemlock could be selectively damaged by wind. Because foliage is present throughout the winter, hemlock may be similarly highly susceptible to ice storm damage. Furthermore, the BRF is hyper-susceptible to wind storm damage because it is a fragmented forest stand characterized by steep slopes. Mou and Warrillow (2000) found a larger number of ice storm gaps on steep slopes, which could result in a fast turnover rate but slow recovery time, which may hinder forest recovery. For the BRF this would further indicate a shift from hemlock to hardwoods. The forest is fragmented due to historical logging of the surrounding forest, which has resulted in second- or third-growth hardwood forests. This could presumably have increased seed rain of hardwoods. Also, anthropogenic land-uses like logging and agriculture create sharp height and density differences along the margins of areas, which cause surviving old-growth stands to project above their surroundings (Foster 1988a), making them more susceptible to windthrow because the largest trees are those most likely to snap (Webb 1988).

Influences on hemlock specifically could also change compositional balance in this forest. For example, deer overpopulation in New England may be affecting the BRF specifically as the deer may preferentially browse on hemlock (Mann et al. unpublished) The effects of this preferential browsing has been documented in other forests to reduce the amount of advance regeneration, putting in question the long-term status of hemlock in these forests (Whitney 1984). A further threat could be the northward spread from southern New England of the introduced hemlock wooly adelgid (*Adelges tsugae*) from Asia, which severely defoliates hemlock, causes high mortality, and indirectly reduces both advance regeneration and the seedbank of this species, which could have serious effects on hemlock-dominated forest (Orwig and Foster 1998).

Conclusions

It has been suggested that the BRF may be experiencing a change in disturbance regime from fire to wind and a corresponding change from hemlock and pine dominance to an increasing contingent of northern hardwood species (Mann et al., unpublished). Four years after the 1998 ice storm, half of the gaps studied showed greater importance of hemlocks while in the other half northern hardwood species were more important. No conclusions can be drawn on gap capture at this early stage of forest regeneration, but overall hemlock dominance of the forest does not seem to be immediately threatened. There are, however, a number of plausible scenarios that could shift the balance between hemlock and northern hardwood species in the Battell Research Forest.

The results of this study of gaps in the Battell Research Forest created by the 1998 ice storm contribute to the small body of literature on the early cohort of forest regeneration after disturbance, and after ice storms in particular. This study was important because by having 2 years of data, the *process* of forest regeneration could be studied. The work can be continued because the gaps, gap plots, and seedlings and saplings within the plots are all permanently marked. Future work could include further descriptive study of the 1998 ice storm gaps. Additionally, if one were to relocated old gaps created by the Great Appalachian Windstorm of 1950, one could examine the understory that had been reinitiated, to see what the compositional balance between hemlocks and northern hardwoods species was there. This would further serve to investigate Mann et al.'s hypothesis that northern hardwoods may be slowing gaining dominance over hemlock.

If one were to paramatize a model to predict the future composition of the Battell Research Forest, there are four salient findings from this study that would contribute to that effort:

(1) Significant density decreases, presumably due to mortality, already occur within the first 4 growing seasons after gap formation.

(2) Mortality rates are higher for shade intolerant species than either species of intermediate tolerance or shade tolerant species.

(3) The mortality rate of northern hardwood species is higher than that of hemlock.

(4) There is a high degree of variability among gaps, which stems from a number of factors of varying predictability, including characteristics of the gap itself (size, slope, orientation), local seed rain, good seed years, subsequent disturbance effects, differential herbivory, mortality rates, species longevity, etc.

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Table 1. Site characteristics of each gap as measured in 2001. Intact forest plots were $25m^2$.

Gap	Gap area (m^2)	Slope (o)	Aspect (o)	Number of gapmakers	Total # of $0.25m^2$ plots sampled in 1999	Total # of $1m^2$ plots sampled in 2001	Total # of intact forest plots sampled in 2001
1	528	12	35	10	20	9	3
2	511	43	75	12	20	11	3
3	402	43	65	7	20	11	3
5	650	44	30	7	20	8	3

Table 2: Rank abundance of seedling densities in 1998 ice storm gaps in 1999 and 2001. Gaps are ranked from 1 (highest density) to 4 (lowest density). Mean seedling density values ± S.E. are given.

Gap	1999 seedling density	2001 seedling density	Ranking 1999	Ranking 2001
1	17.20 (±4.28)	10.78 (±4.92)	1	1
2	7.60 (±3.27)	1.64 (±0.70)	4	4
3	8.20 (±2.62)	4.55 (±1.21)	3	2
5	10.00 (±2.40)	2.13 (±0.90)	2	3

Table 3. The presence and absence of species found in the Battell Research Forest by Mann et al. (unpublished), Gilbert (2000), and Jewell (current study). Mann and Jewell (intact forest) species were those found in undisturbed forest, while Gilbert and Jewell (gaps) species were those found in 1998 ice-storm gaps. Species marked by (a) were found but not in the plots sampled. Species richness is included.

Woody plant species	**Mann**	**Gilbert**	**Jewell (gaps)**	**Jewell (intact forest)**
Year sampled	**1991**	**1999**	**2001**	**2001**
Eastern hemlock *(Tsuga canadensis)*	X	X	X	X
Red pine *(Pinus resinosa)*	X			X
White pine *(Pinus strobus)*	X	X[a]	X	X
Red spruce *(Picea rubens)*	X			X
Beech *(Fagus grandifolia)*	X	X[a]	X	X
Black birch *(Betula lenta)*	X		X	X
Yellow birch *(Benta lutea)*	X	X	X	X
Paper birch *(Betula papyrifera)*	X	X	X	X
Red maple *(Acer rubrum)*	X	X	X	X
Sugar maple *(Acer saccharum)*	X	X[a]	X	X
Eastern mountain maple *(Acer spicatum)*	X	X		X
Striped maple *(Acer penslyvanicum)*	X	X	X	X
Silver maple *(Acer saccharinum)*		X[a]		X
Swamp oak *(Quercus bicolor)*				X
Northern red oak *(Quercus rubra)*	X			X
White ash *(Fraxinus americana)*	X			
Pin cherry *(Prunus pensylvanica)*	X	X	X	X
Eastern hornbeam *(Ostrya virginiana)*	X			
Quaking aspen *(Populus tremuloides)*	X			
Shagbark hickory *(Carya ovata)*	X			
Butternut *(Juglans cinerea)*	X			
Common witch-hazel *(Hamamelis virginiana)*	X			X
American basswood *(Tilia americana)*				X
American elm *(Ulmus americana)*				X
Juneberry (*Amelanchier* spp)				X
Species richness	20	11	10	20

Table 4. The presence and absence of species found in the 1998 ice storm gaps and intact forest at each site in 2001. Species richness is included.

Woody plant species	**Site 1**		**Site 2**		**Site 3**		**Site 5**	
	Gap	**Intact forest**	**Gap**	**Intact forest**	**Gap**	**Intact forest**	**Gap**	**Intact forest**
Eastern hemlock *(Tsuga canadensis)*	X	X	X	X	X	X	X	X
White pine *(Pinus strobus)*		X	X	X		X		
Beech *(Fagus grandifolia)*	X							
Yellow birch *(Benta lutea)*	X	X	X	X	X	X	X	X
Paper birch *(Betula papyrifera)*	X		X	X	X	X		X
Red maple *(Acer rubrum)*	X	X		X	X	X		X
Sugar maple *(Acer saccharum)*	X	X		X	X	X		
Eastern mountain maple *(Acer spicatum)*								X
Striped maple *(Acer penslyvanicum)*	X	X		X	X	X	X	X
Silver maple *(Acer saccharinum)*						X		
Swamp oak *(Quercus bicolor)*		X		X				
Northern red oak *(Quercus rubra)*		X						X
Pin cherry *(Prunus pensylvanica)*	X		X	X			X	X
American elm *(Ulmus americana)*				X				
Juneberry *(Amelanchier* spp.)		X						
Species richness	8	9	5	10	6	8	4	8

Table 5: Mean seedling densities of hemlock, northern hardwood species (grouped together), red maple, and *Betula* spp. Values are mean densities (± 1 S.E.) for 1998 ice storm gaps in 1999 and 2001 and in the intact forest in 2001.

Species	Gap	1999 gap	2001 gap	2001 intact forest
Hemlock	1	2.40 (±1.87)	1.22 (±0.25)	0.25 (±0.13)
	2	1.00 (±0.64)	0.2727 (±0.20)	0.01 (±0.01)
	3	1.40 (±0.88)	2.27 (±0.87)	0.16 (±0.08)
	5	2.60 (±1.10)	1.25 (±0.49)	0.48 (±0.16)
Northern hardwoods	1	14.80 (±3.15)	9.56 (±4.37)	0.60 (±0.40)
	2	6.60 (±2.74)	1.18 (±0.55)	0.77 (±0.36)
	3	6.80 (±2.36)	2.27 (±0.82)	0.65 (±0.33)
	5	7.40 (±2.14)	0.88 (±0.52)	0.68 (±0.42)
Red maple	1	11.60 (±2.71)	7.56 (±4.11)	0.44 (±0.38)
	2	0.60 (±0.33)	0.00	0.09 (±0.06)
	3	1.80 (±0.98)	0.18 (±0.12)	0.17 (±0.12)
	5	3.60 (±0.91)	0.00	0.03 (±0.03)
***Betula* spp.**	1	2.80 (±1.09)	1.33 (±0.53)	0.03 (±0.01)
	2	4.20 (±2.64)	0.91 (±0.53)	0.28 (±0.13)
	3	3.80 (±0.98)	1.27 (±0.65)	0.13 (±0.03)
	5	2.80 (±1.09)	0.63 (±0.50)	0.23 (±0.17)

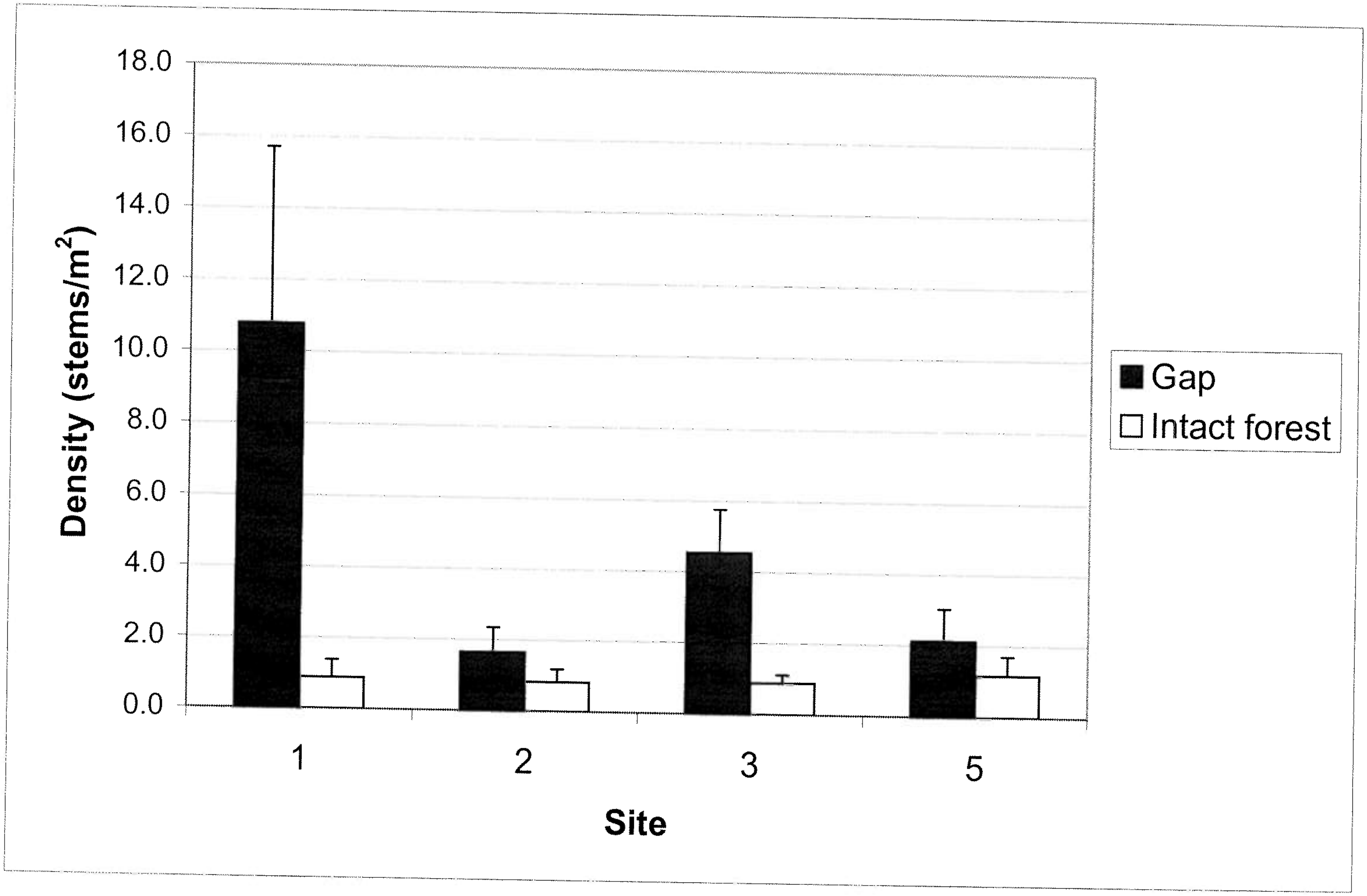


Figure 1: Mean seedling stem density in the gap and the intact forest at each site in 2001. Sample sizes can be found in Table 1. Error bars are 1 S.E.

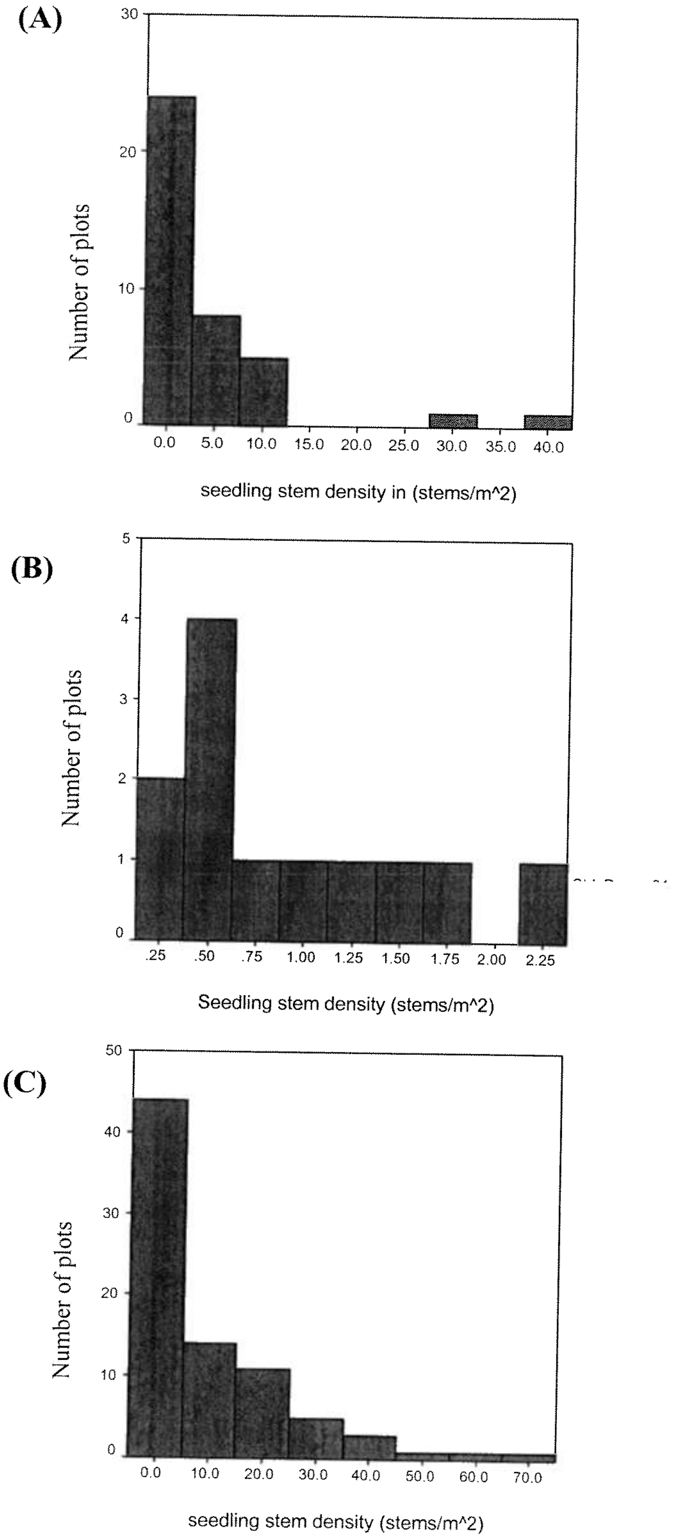


Figure 2: Histograms of seedling stem densities in each plot. (A) 2001 seedling densities of 1998 ice storm gaps. (B) 2001 intact forest plot densities. (C) 1999 seedling densities of 1998 ice storm gaps.

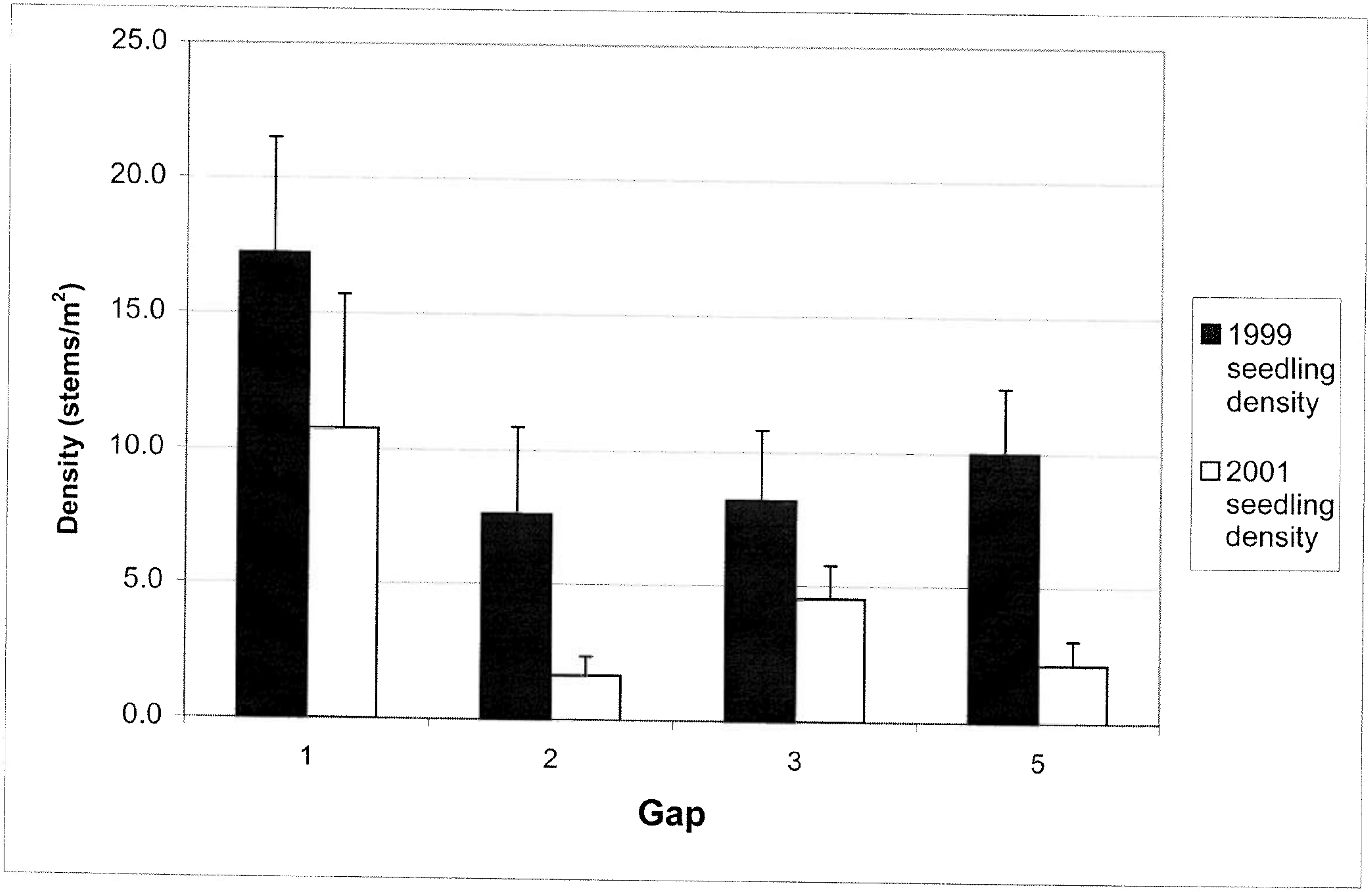


Figure 3: Mean seedling stem densities in 1999 and 2001 in 1998 ice storm gaps. Sample sizes can be found in Table 1. Error bars are 1 S. E.

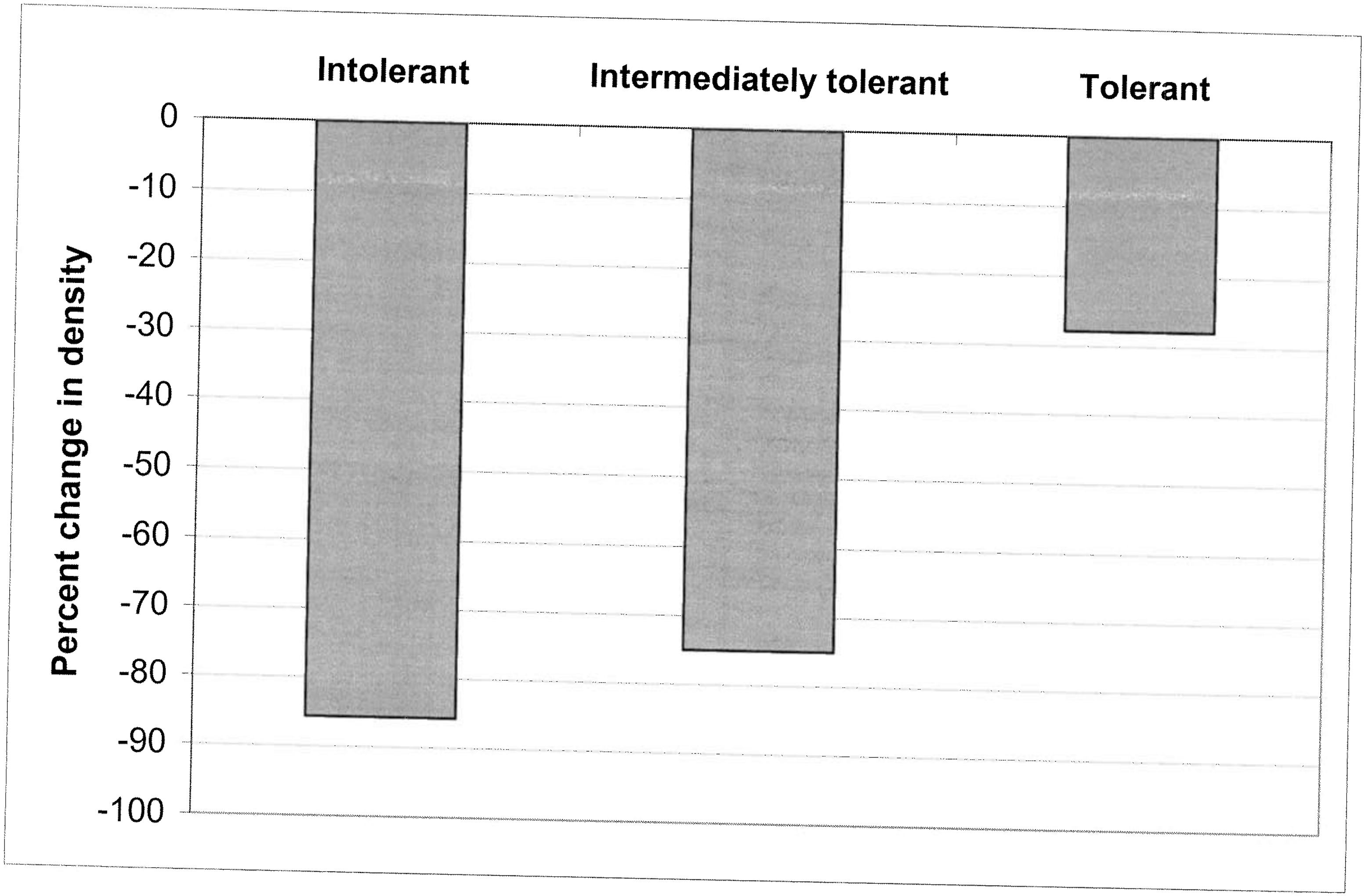


Figure 4: Percent change in density of seedlings in gaps between 1999 and 2001 by shade tolerance level. Intolerant species are paper birch and pin cherry; intermediately tolerant species are red maple and *Betula* spp.; the shade tolerant species was hemlock. Values used are the percent change in density averaged across gaps for each species.

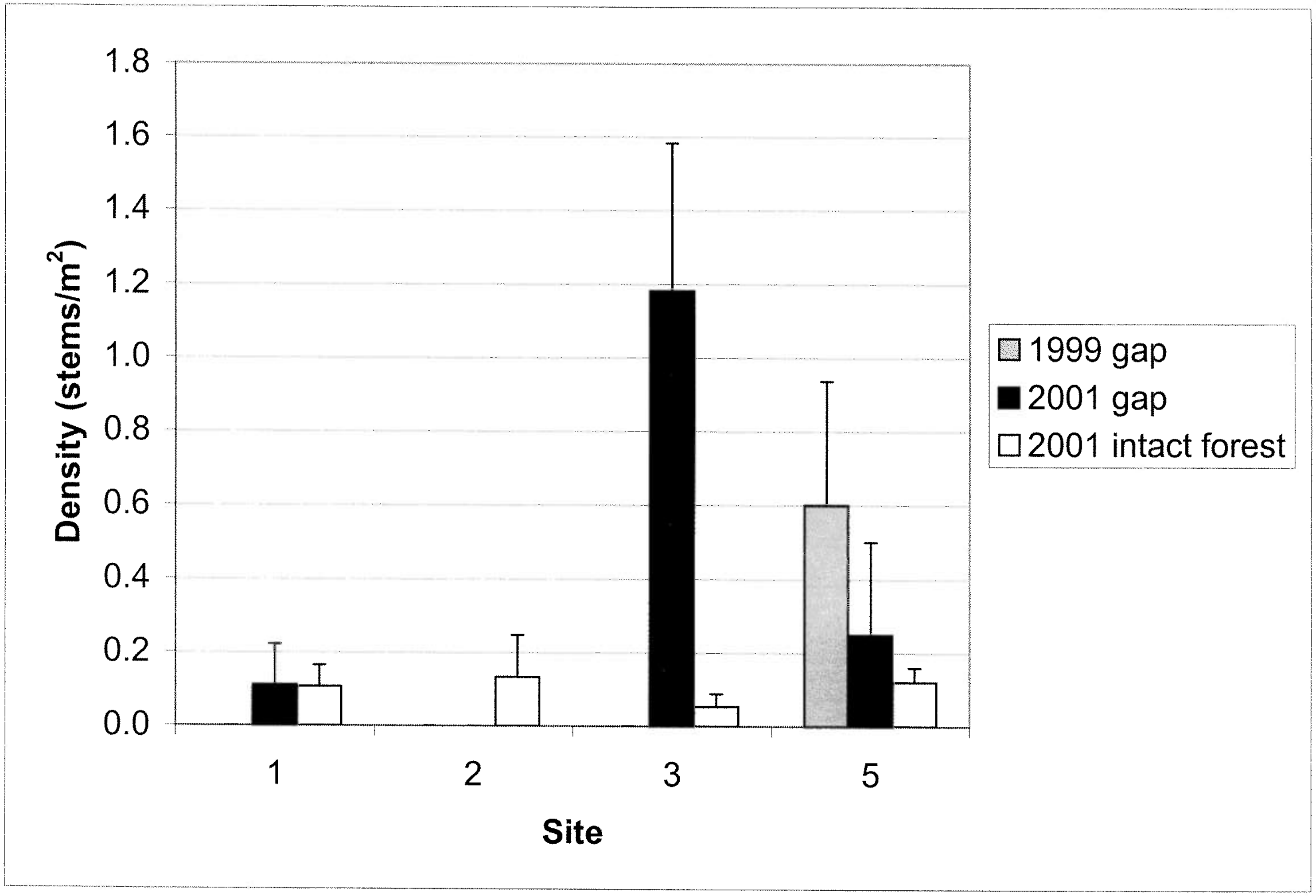


Figure 5: Mean sapling density at each site. 1998 ice storm gaps were sampled in 1999 and 2001, while intact forest plots were sampled in 2001. Sample sizes can be found in Table 1. Error bars are 1 S.E.

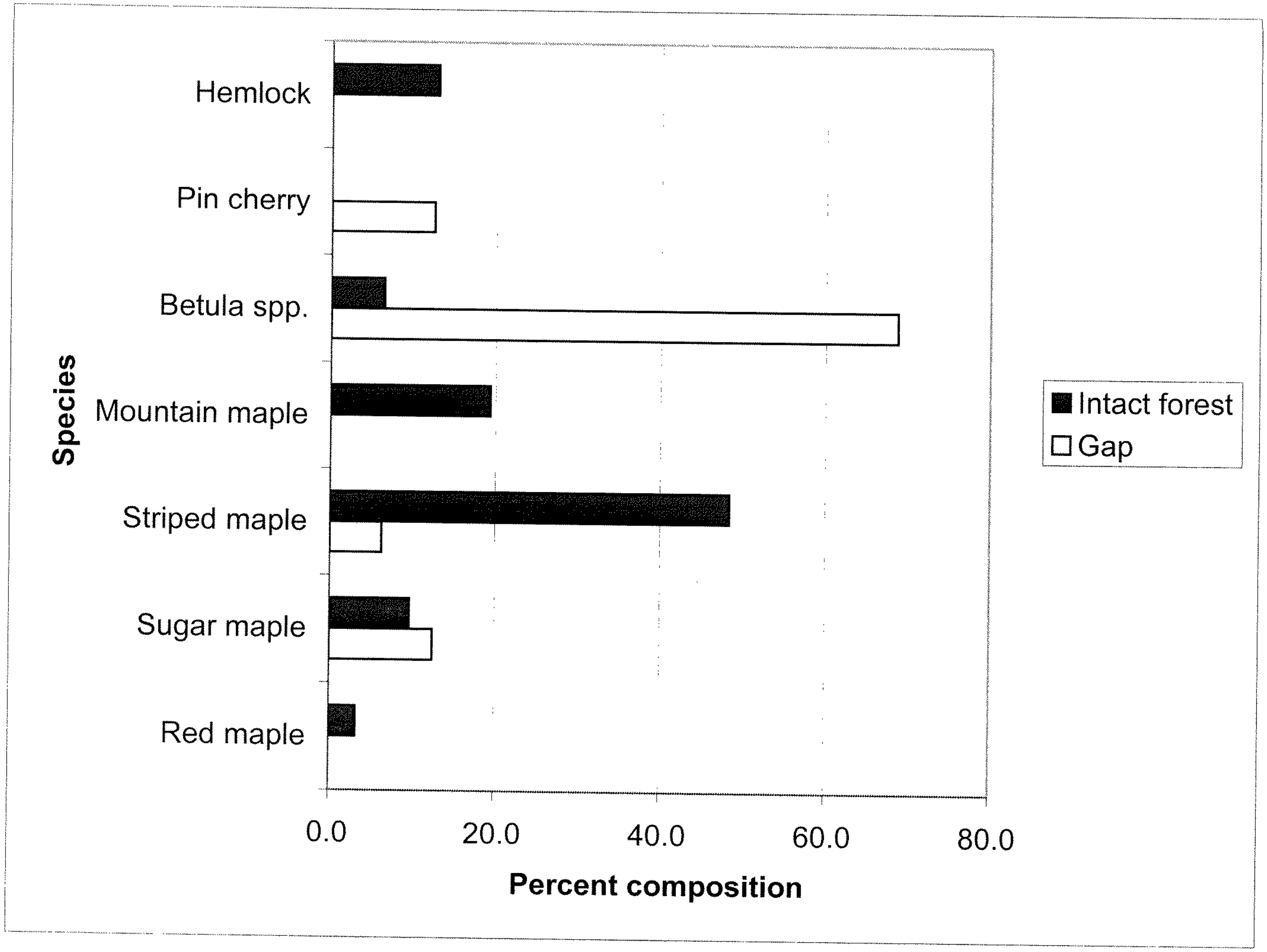
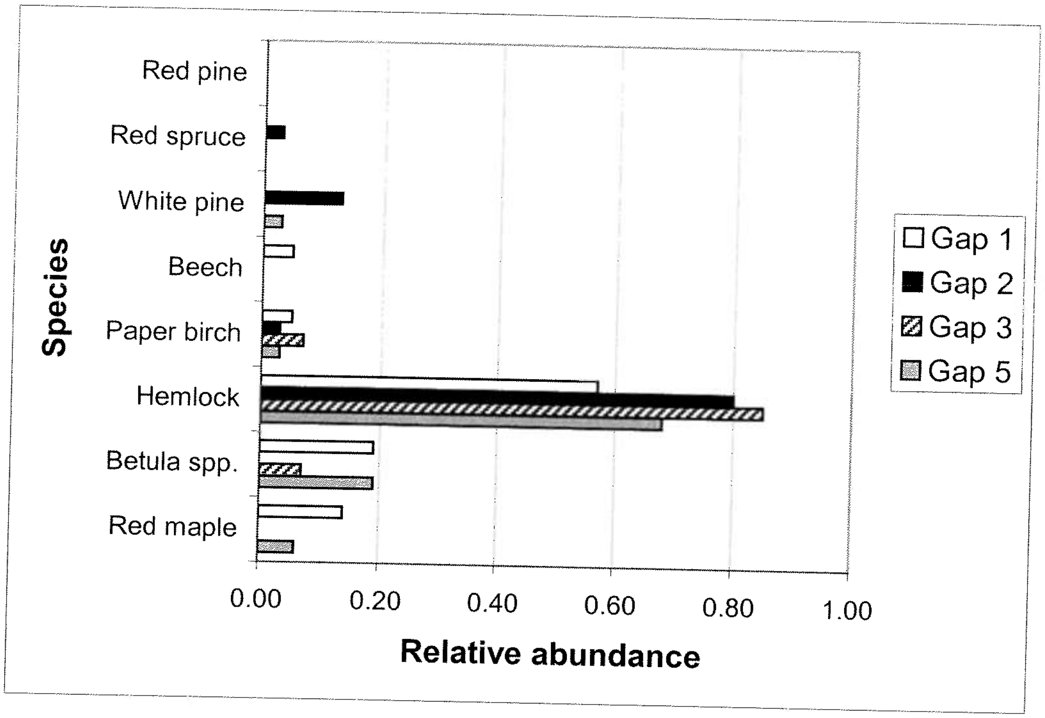


Figure 6: Sapling composition of gaps and intact forest in 2001. Total numbers of saplings for each site were used rather than the mean of each site. Thus, error bars are not included.

(A)



(B)

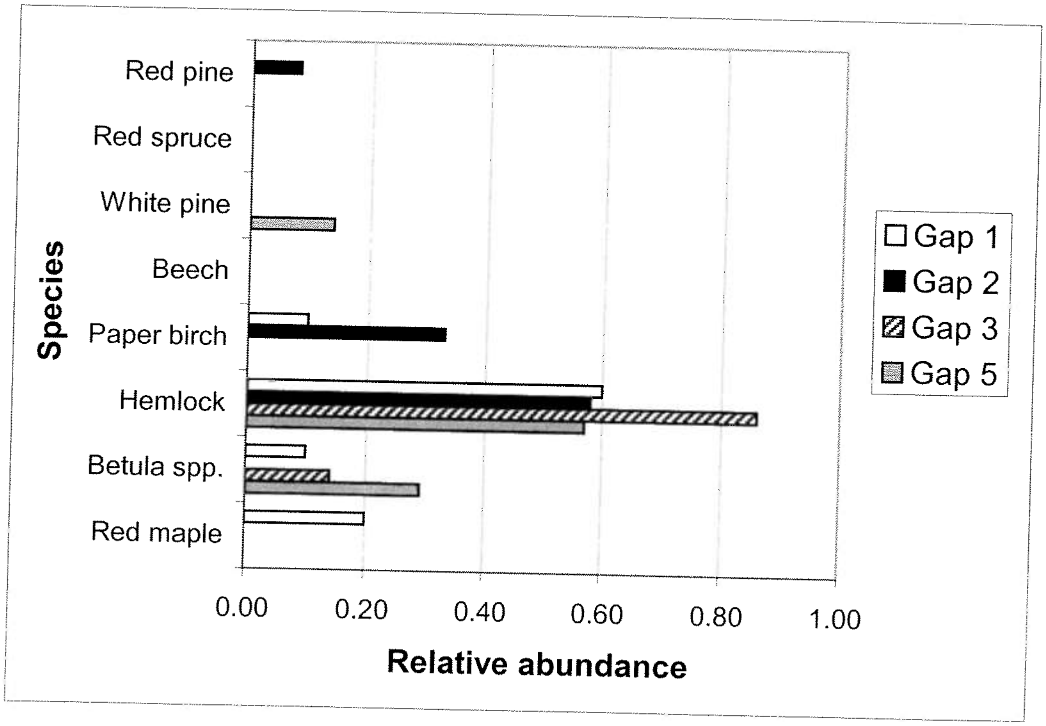


Figure 7: The composition by relative abundance of trees at each site in 2001. (A) Composition of extant trees at the perimeter of a gap (within 3m of the gap). (B) Composition of the gapmakers of each gap, as identified by trunks.

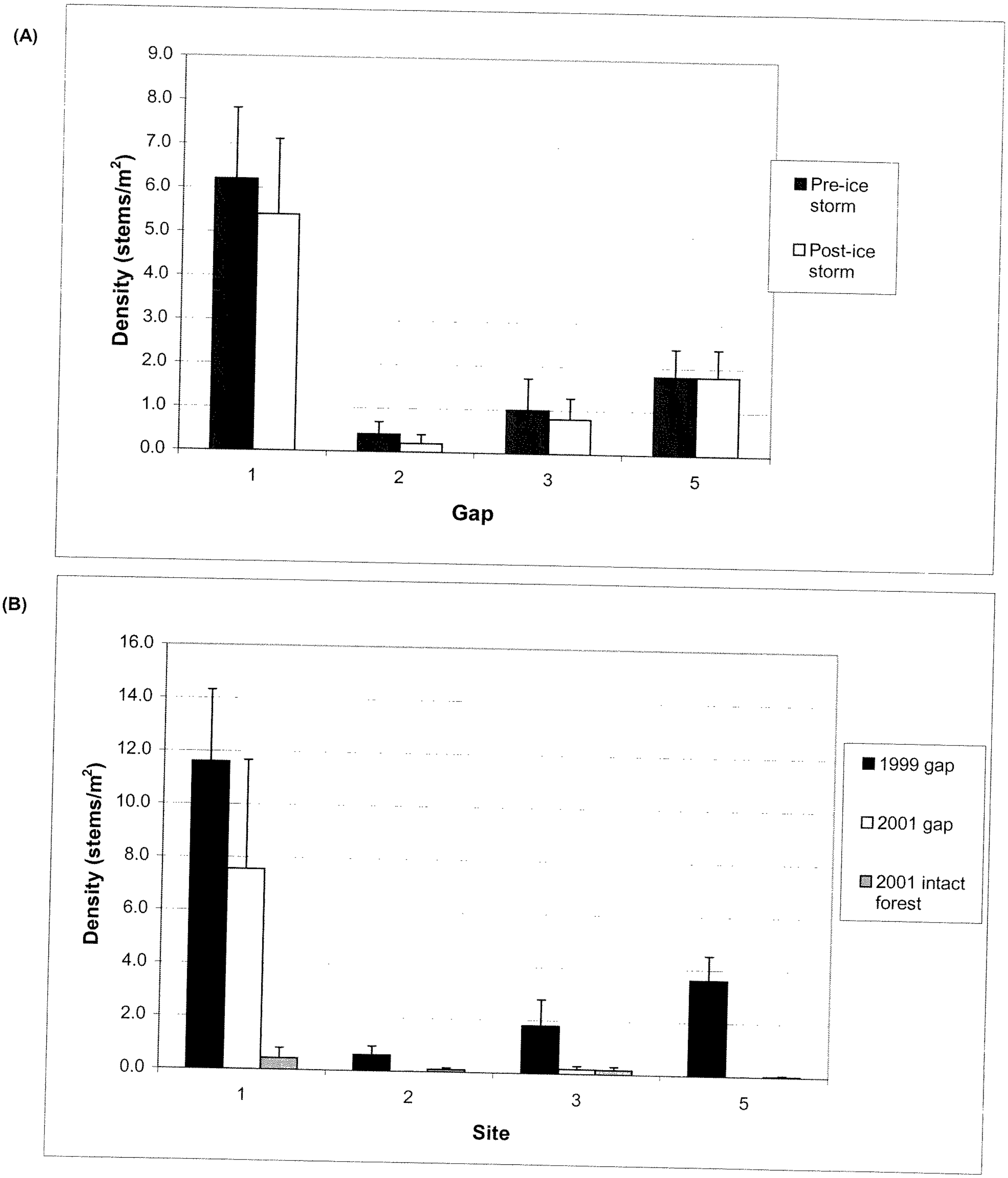


Figure 8: Red maple seedling densities. (A) Red maple seedlings sampled in 1999 were grouped by establishment time. (B) Red maple seedlings were sampled in 1998 ice storm gaps in 1999 and 2001, and in intact forest plots in 2001. Sample sizes can be found in Table 1. Error bars are 1 S.E.

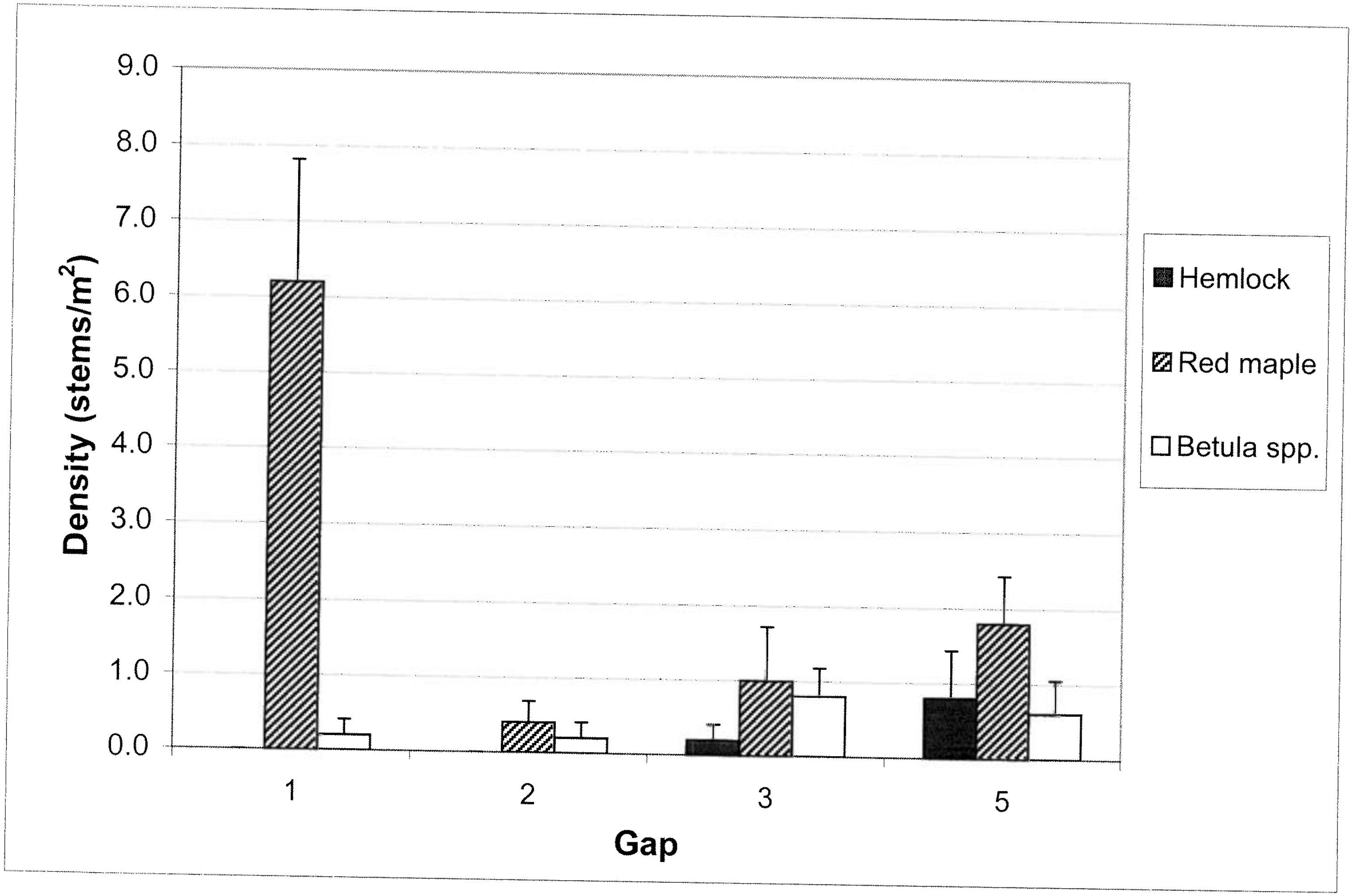


Figure 9: Density of seedlings established before the 1998 ice storm, from 1999 data. Hemlock, red maple, and *Betula* spp are included. Sample sizes can be found in Table 1. Error bars are 1 S.E.

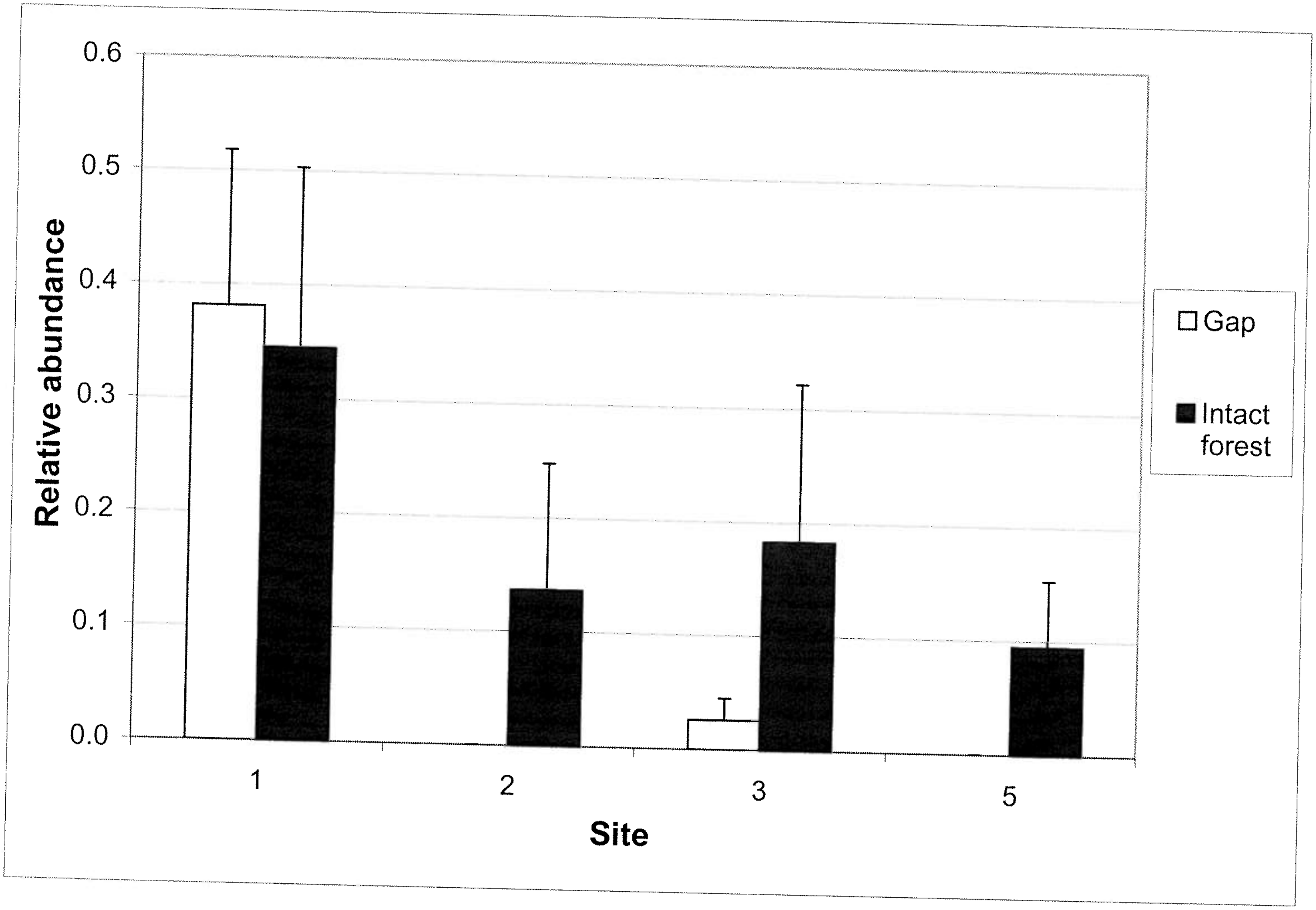


Figure 10: Mean relative abundance of red maple seedlings in gaps and intact forest for each site. Values given are the mean relative abundance, or the proportion of red maple stems of all stems per plot. Sample sizes can be found in Table 1. Error bars are 1 S.E.

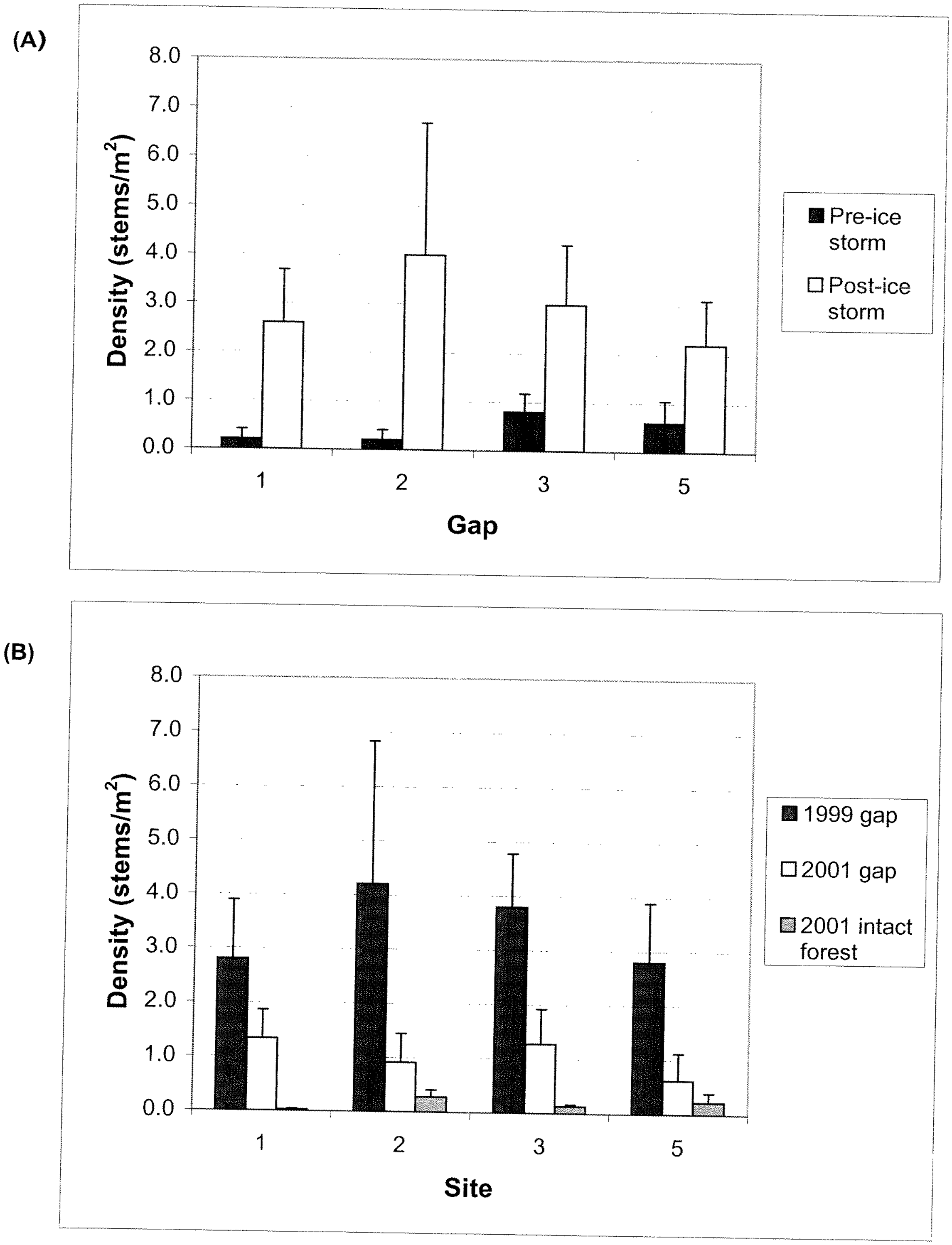


Figure 11: *Betula* spp. seedling densities. Yellow birch and black birch seedlings sampled were grouped together for analysis under *Betula* spp. (A) *Betula* spp. sampled in 1999 was grouped by establishment time. (B) *Betula* spp. was sampled in 1998 ice storm gaps in 1999 and 2001, and in intact forest plots in 2001. Sample sizes can be found in Table 1. Error bars are 1 S.E.

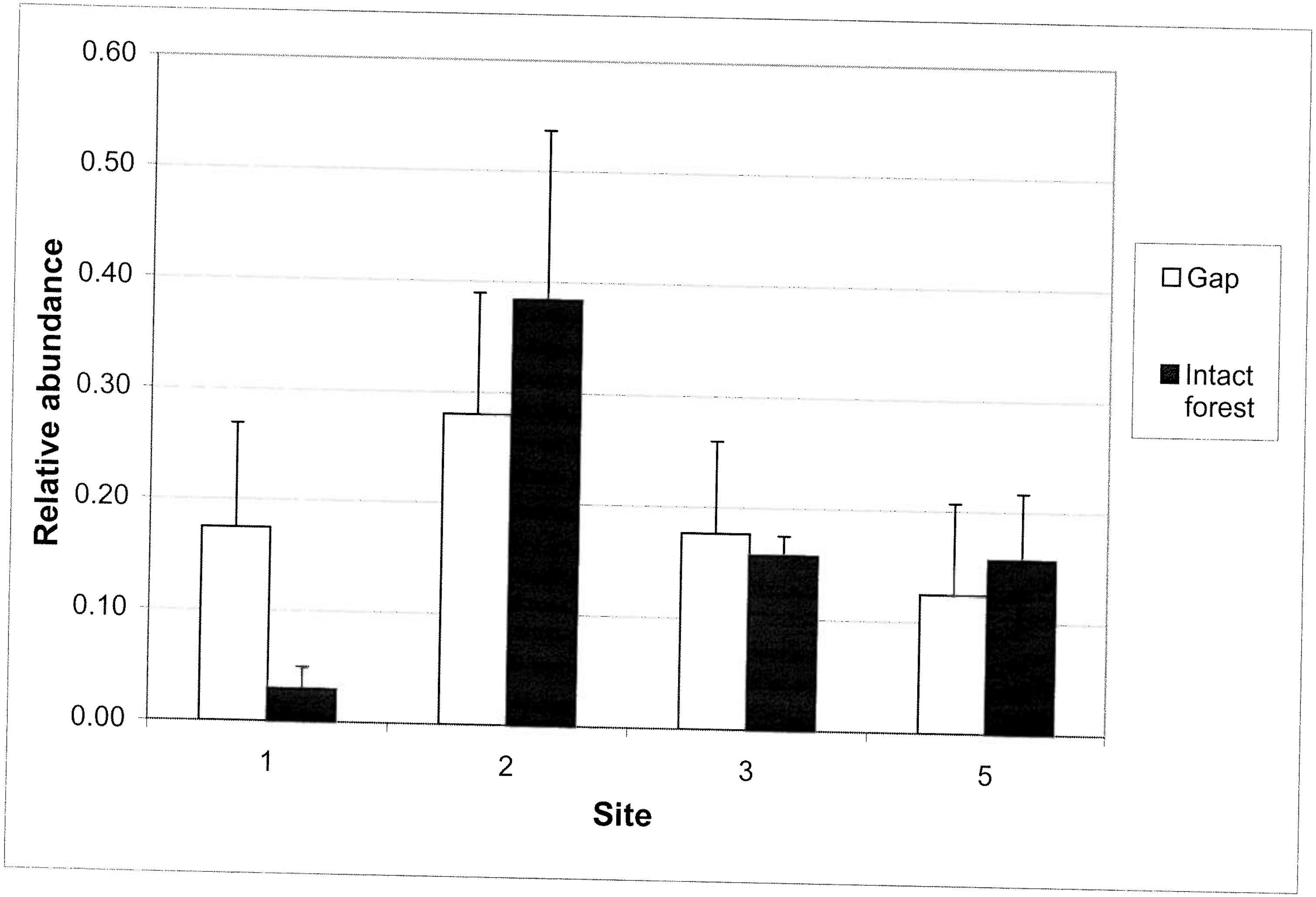


Figure 12: Relative abundance of *Betula* spp. seedlings in gaps and intact forest for each site. Values given are the mean relative abundance, or the proportion of *Betula* spp. stems of all stems per plot. Sample sizes can be found in Table 1. Error bars are 1 S.E.

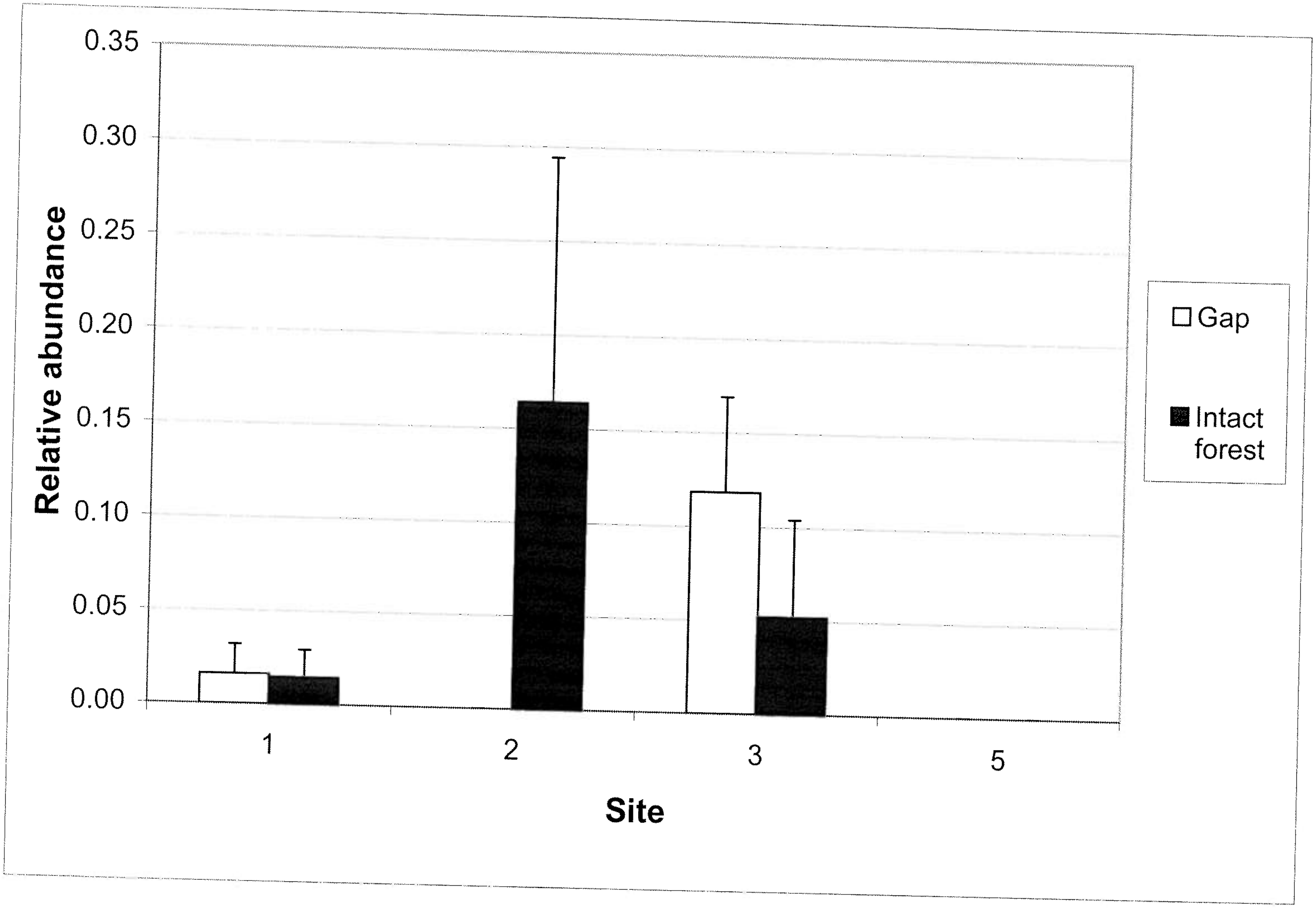


Figure 13: Relative abundance of sugar maple seedlings in gaps and intact forest for each site. Values given are the mean relative abundance, or the proportion of sugar maple stems of all stems per plot. Sample sizes can be found in Table 1. Error bars are 1 S.E.

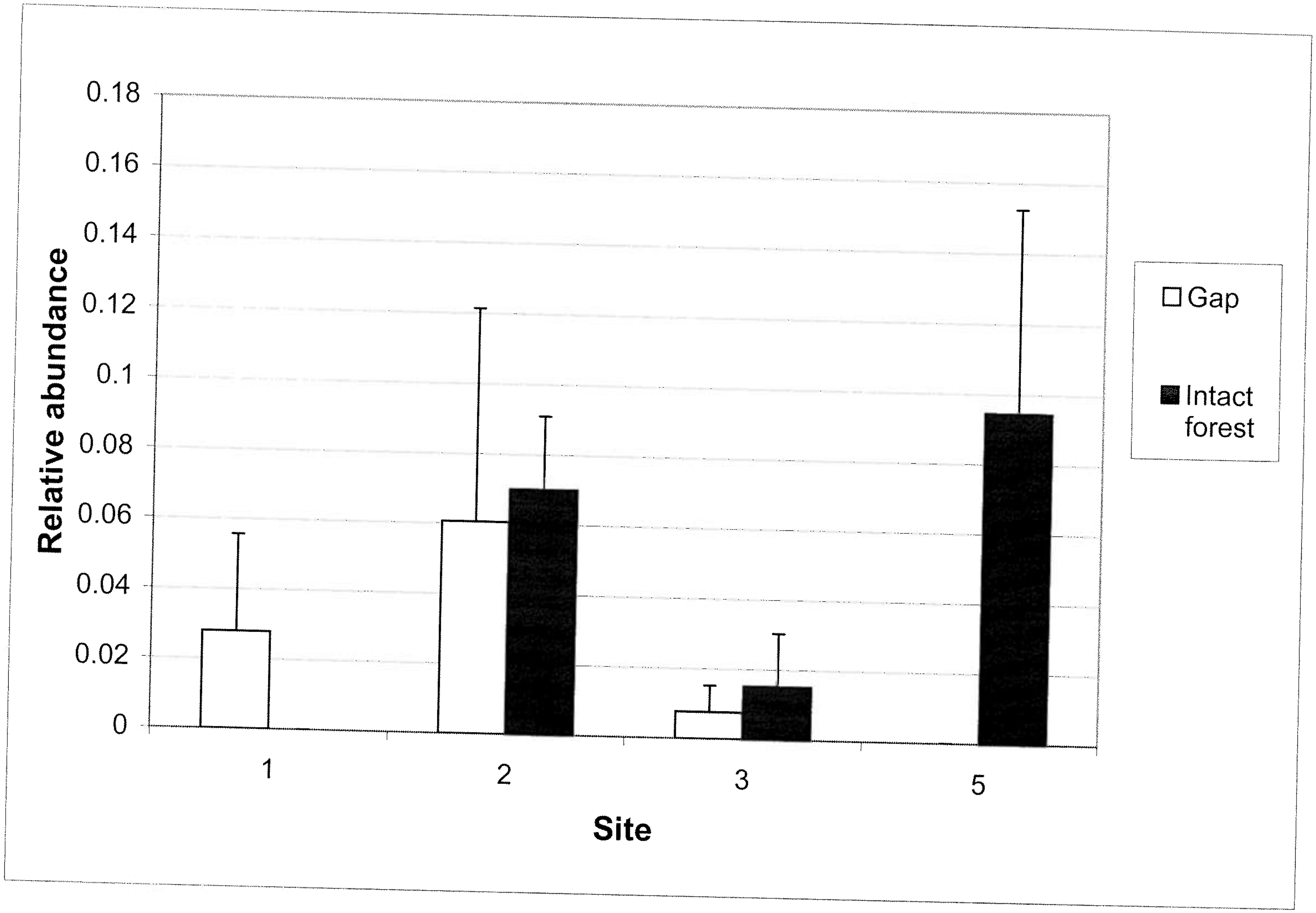


Figure 14: Relative abundance of paper birch seedlings in gaps and intact forest for each site. Values given are the mean relative abundance, or the proportion of paper birch stems of all stems per plot. Sample sizes can be found in Table 1. Error bars are 1 S.E.

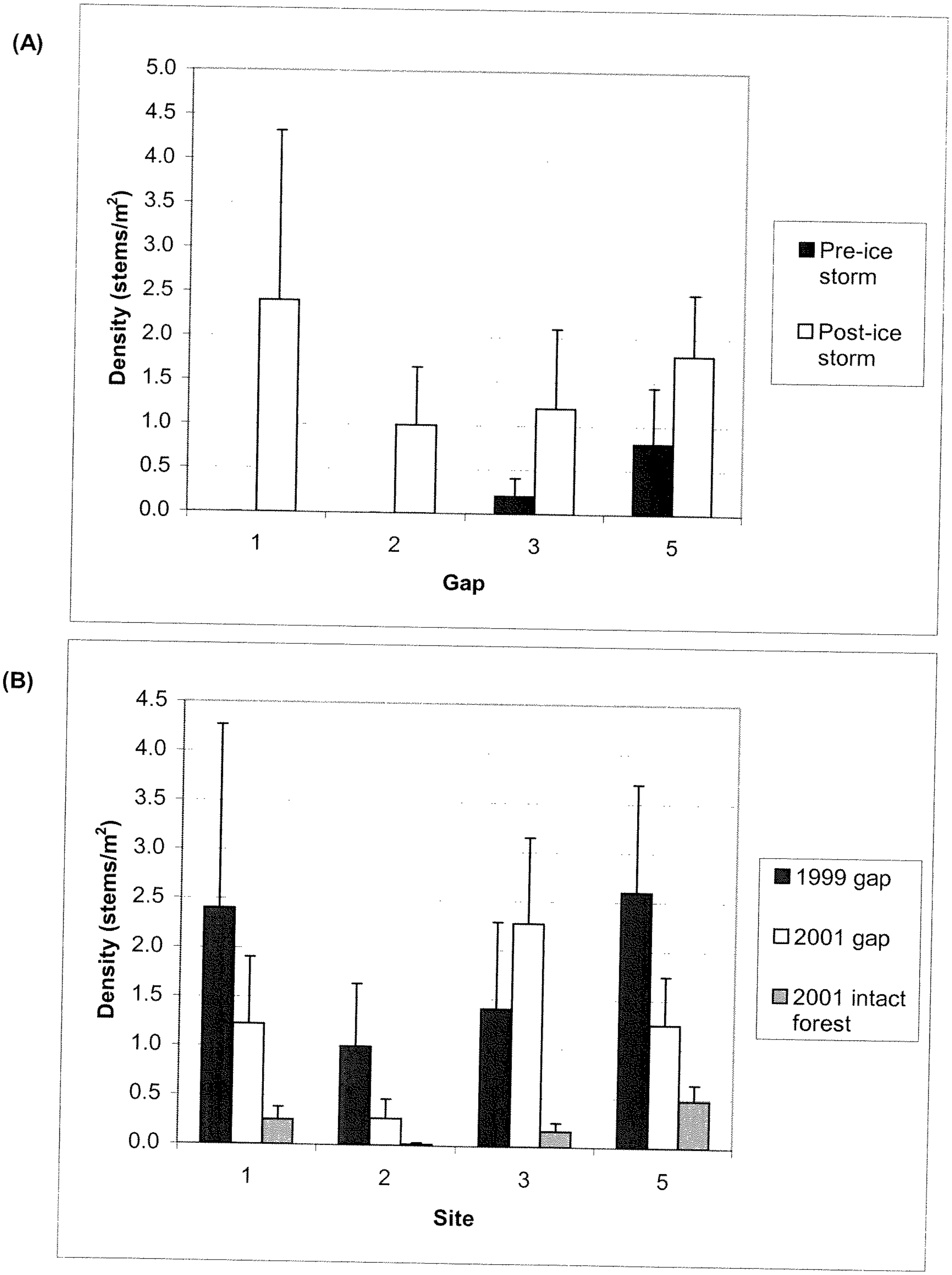


Figure 15: Hemlock seedling densities. (A) Hemlock seedlings sampled in 1999 were grouped by establishment time (pre or post 1998 ice storm). (B) Hemlock seedlings were sampled in 1998 ice storm gaps in 1999 and 2001, and in intact forest plots in 2001. Sample sizes can be found in Table 1. Error bars are 1 S.E.

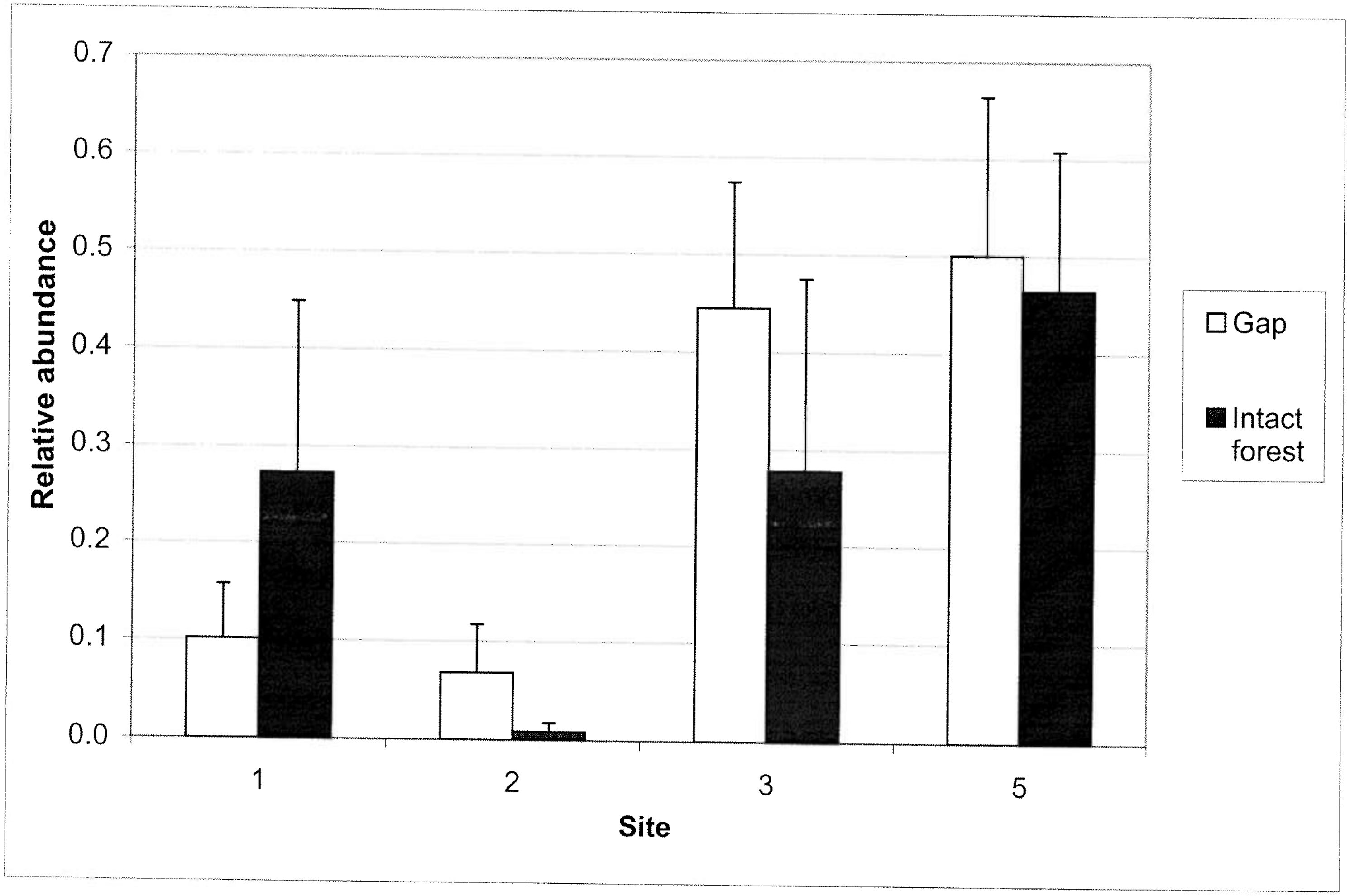


Figure 16: Relative abundance of hemlock seedlings in gaps and intact forest for each site. Values given are the mean relative abundance, or the proportion of hemlock stems of all stems per plot. Sample sizes can be found in Table 1. Error bars are 1 S.E.

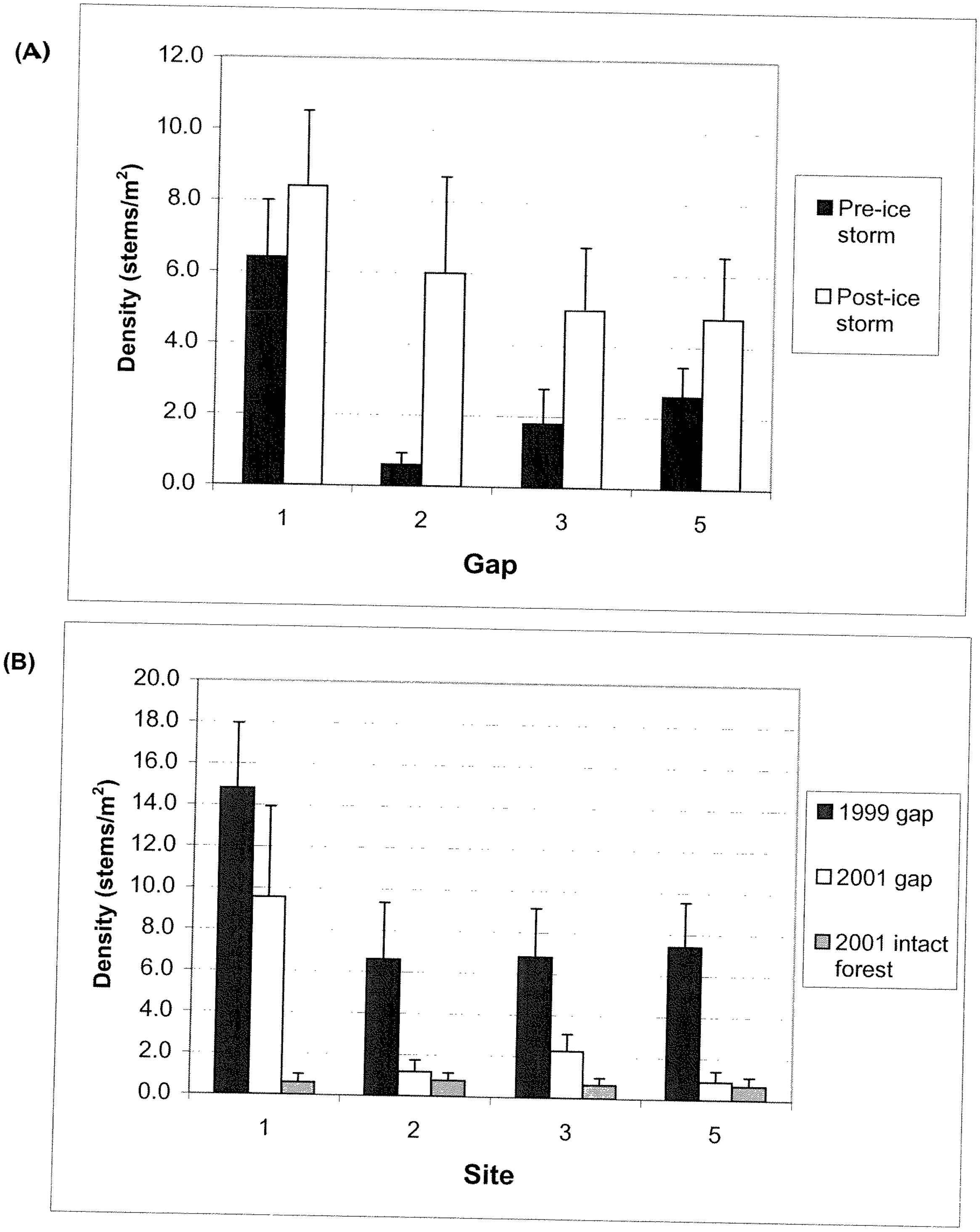


Figure 17: Northern hardwood species seedling densities. See methods for species list. (A) Northern hardwood species sampled in 1999, grouped by establishment time. (B) Northern hardwood seedlings sampled in 1998 ice storm gaps in 1999 and 2001, and in intact forest plots in 2001. Sample sizes can be found in Table 1. Error bars are 1 S.E.

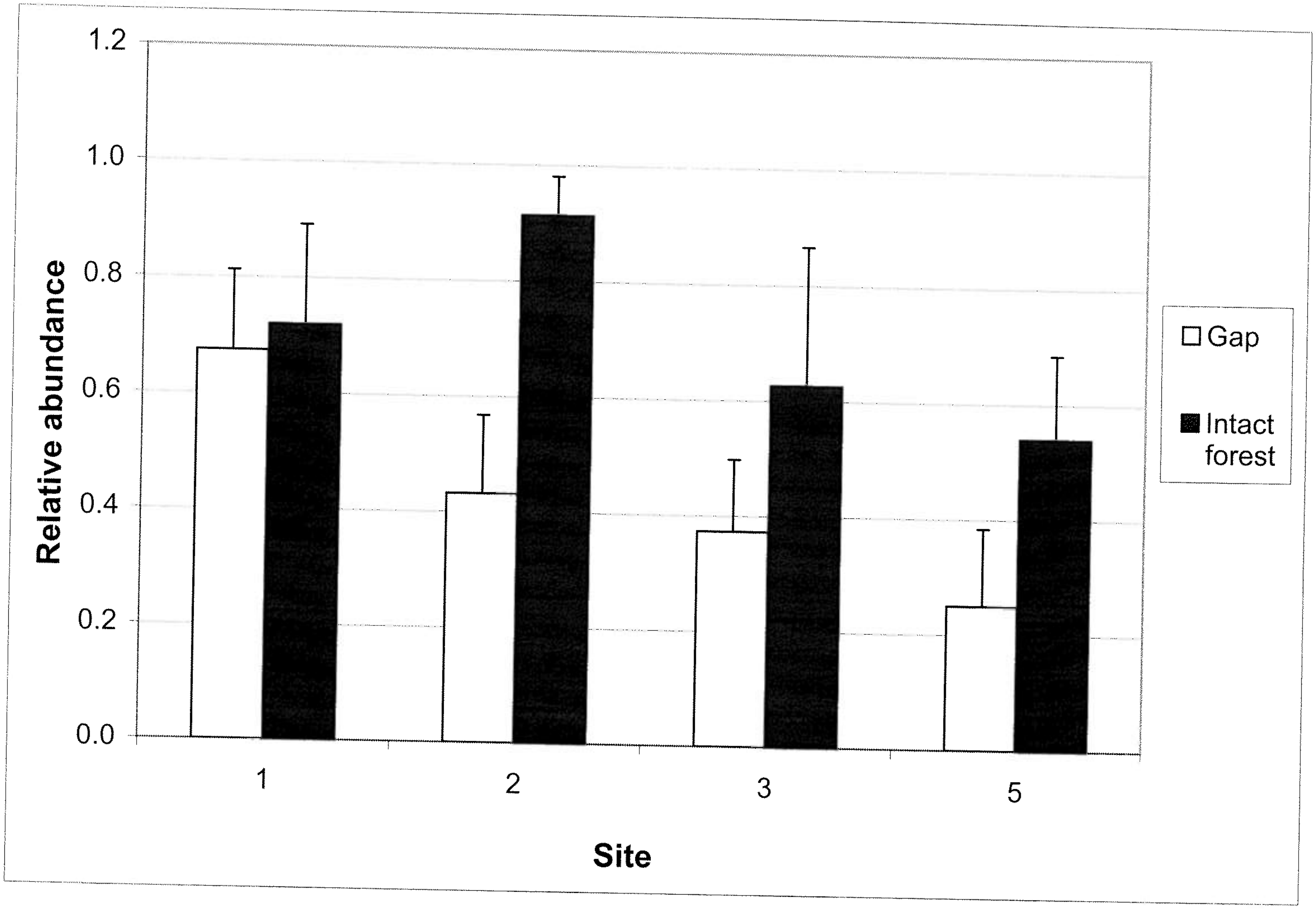


Figure 18: Relative abundance of northern hardwood seedlings in gaps and intact forest for each site. Values given are the mean relative abundance, or the proportion of hardwood spp. stems of all stems per plot. Sample sizes can be found in Table 1. Error bars are 1 S.E.

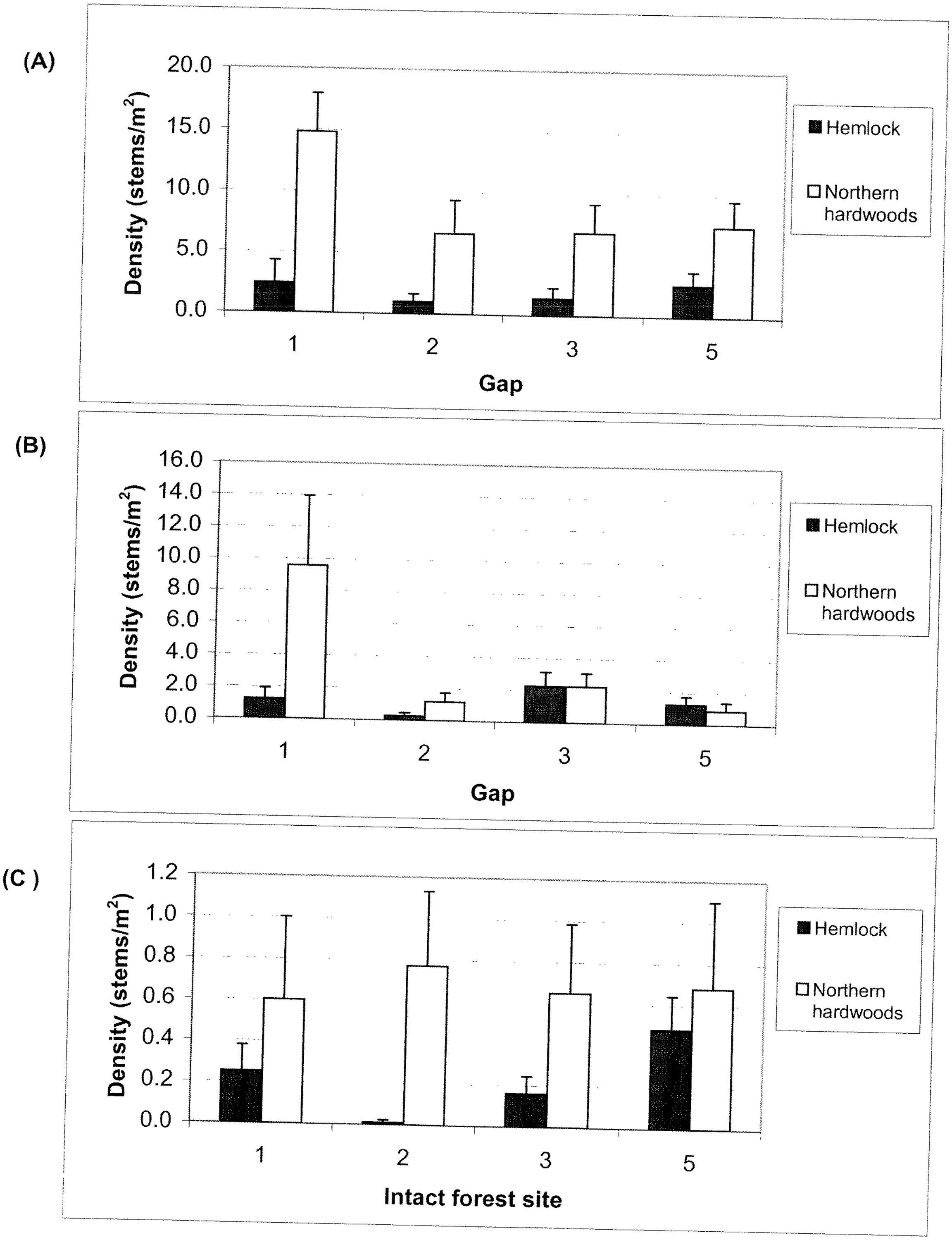


Figure 19: Mean seedling density of hemlock and northern hardwood species. (A) Mean seedling densities in 1998 ice storm gaps as sampled in 1999. (B) Mean seedling densities in 1998 ice storm gaps as sampled in 2001. (C) Mean seedling density in intact forest plots sampled in 2001. Sample sizes can be found in Table 1. Error bars are 1 S.E.

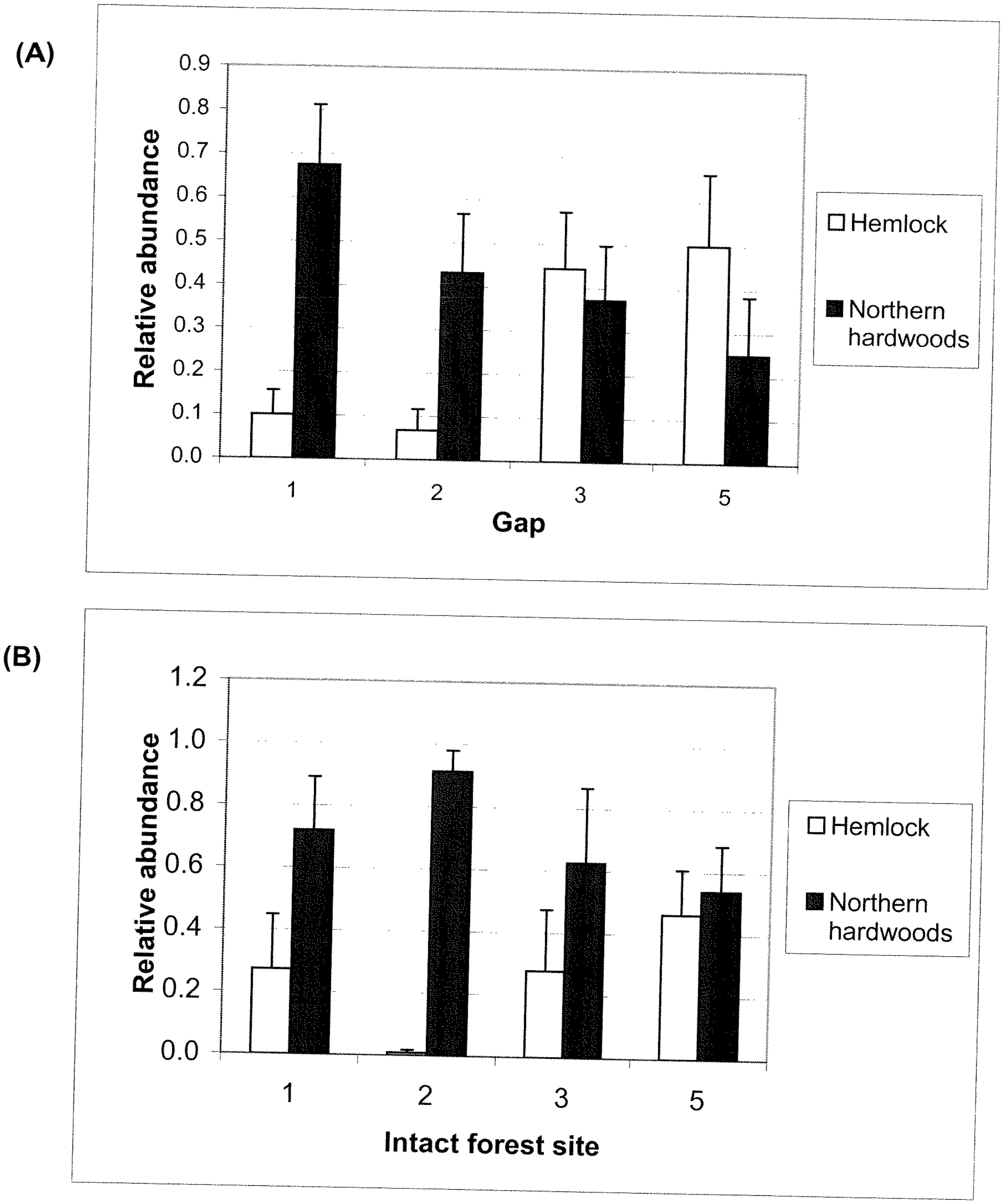


Figure 20: Relative abundance of hemlocks and northern hardwood species. Values are given as mean relative abundance, or the proportion of stems of a species of all stems per plot. (A) Relative abundance of hemlock and northern hardwood seedlings in 1998 ice storm gaps. (B) Relative abundance of hemlock and northern hardwood seedlings in intact forest plots in 2001. Sample sizes can be found in Table 1. Error bars are 1 S.E.

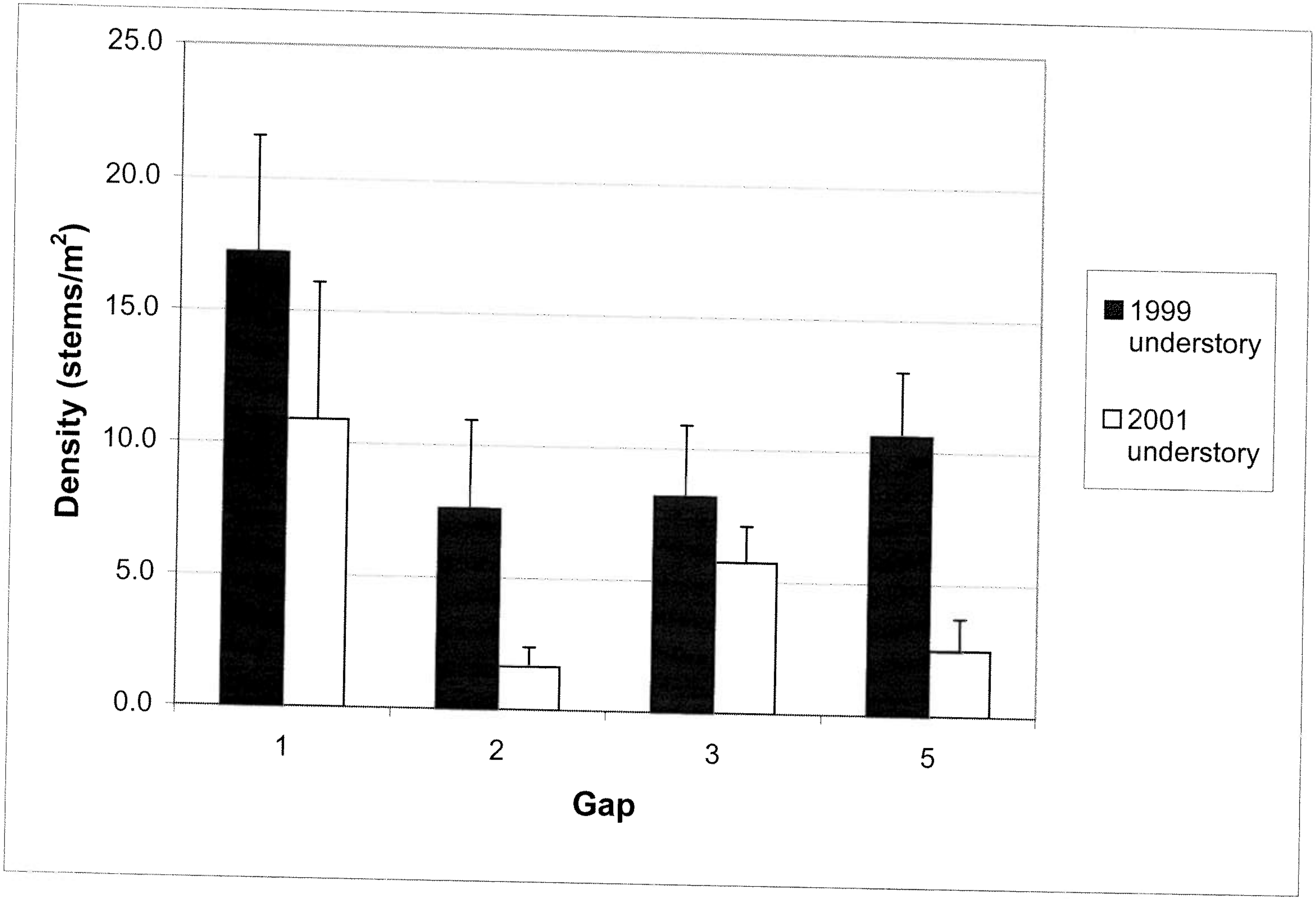


Figure 21: Mean understory stem densities for each gap. Understory includes all seedlings and saplings sampled. 1998 ice storm gaps were sampled in 1999 and 2001. Sample sizes can be found in Table 1. Error bars are 1 S.E.