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SEED BANK DYNAMICS WITHIN A METAPOPULATION FRAMEWORK: A STUDY OF AN ANT-DISPERSED SPECIES

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ABSTRACT

SEED BANK DYNAMICS WITHIN A METAPOPULATION FRAMEWORK: A STUDY OF AN ANT-DISPERSED SPECIES

By

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Questions. How do spatial and temporal landscape dynamics, including past disturbance, affect the distribution of the seed bank of an early-succession species? Do these factors ultimately influence above-ground subpopulation persistence within a metapopulation framework?

Location. Granite-gneiss outcrops within mixed hardwood-conifer forest in Michigan, USA

Methods. We studied the distribution of the *Capnoides sempervirens* seed bank on outcrops and within the forest matrix in relation to landscape and physiographic (*n* = 517). Above-ground plant persistence (*n* = 144) in relation to landscape and habitat variables was also investigated.

Results. Seeds were found up to 175 m from outcrops, but seed presence generally decreased with increased distance to outcrops. Areas of recent fire had both increased abundance and greater frequency of occurrence of seeds. Seed presence on outcrops shared no relationship with adult plants, but instead corresponded to increased groundcover at sampling locations.

Conclusions. Results indicated seed distribution is not random but reliant upon spatial and temporal predictors. Increased seed presence in relation to adult-plant habitat demonstrated seed bank distribution has some dependence on distance from source populations and primary disperser activity, but the presence of seeds within the greater forest matrix also indicated reliance on landscape, physiographic, or disturbance-related factors. Seed distribution has the potential to influence subpopulation persistence.

Keywords. Seed bank; Metapopulation; Disturbance; Dispersal mechanisms; *Capnoides sempervirens*

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INTRODUCTION

An examination of metapopulations dynamics includes understanding processes affecting extinction and colonization probabilities for interacting subpopulations (Hanski & Gilpin 1991). To better understand plant population dynamics within a metapopulation framework, it is essential to first examine the spatial and temporal landscape processes that ultimately influence seed distribution and longevity. The distribution of plant subpopulations depends on habitat-specific parameters such as patch size, distance between patches and seed dispersal ability (Jacquemyn et al. 2003). Although the presence of a viable seed bank may largely influence colonization and extinction probabilities, examinations of plant metapopulations often fail to consider the distribution of the dormant seed bank (Bossuyt & Honnay 2006; Husband & Barrett 1996; Plue & Hermy 2012). Suitable habitat patches in heterogeneous landscapes may be finite and vary spatially. The amount of linked habitat may decrease or increase with time (Hanski 1999). Within a plant metapopulation framework, habitat connectivity and the ability to colonize or recolonize suitable habitat may depend on the distribution of a persistent seed bank (Alexander et al. 2012; Eriksson 1996, Freckleton & Watkinson 2002; Husband & Barrett 1996). Because habitat connectivity is crucial to subpopulation persistence, a more complete understanding of the spatial and temporal distribution of dormant seeds provides much needed insight into the mechanisms influencing plant population dynamics in heterogeneous landscapes.

The traditional metapopulation model applied to plants assumes random dispersal of seeds into habitats classified as suitable or unsuitable for germination (Etienne 2000; Levins 1969). Traditional models may not appropriately capture the spatial and temporal distribution of dormant seeds, especially those seeds displaying persistent dormancy strategies. Mechanisms leading to the formation of persistent seed banks within unsuitable habitat create remnant populations in which systems of local populations are maintained despite a local population growth rate <1 (Eriksson 1996). Non-random distribution of seeds as well as the presence of remnant populations of viable seeds may inhibit the risk of extinction within a variable habitat.

Capnoides sempervirens (L.) Borkh., commonly known as rock harlequin or pale corydalis, is a biennial forb native to mid-latitudes of North America that forms persistent populations on rock outcrops. *C. sempervirens* also forms short-lived populations that emerge from the seed bank after canopy-altering fire (Reznicek et al. 2011). Seed banks also form in cracks and small pockets of soil on rock outcrops; thus, *C. sempervirens* has seed banks that are both coupled and uncoupled to disturbance (*sensu* Grubb 1988).

Above-ground plants are most frequently found 1-2 years post fire, but are less common three years after fire. Previous work indicates *C. sempervirens* seeds, which are primarily ant-dispersed, remain viable within the soil seed bank up to 80 years post-fire (Fyles 1989). Seeds have also been documented in old-growth forests some distance from potential source populations (Leckie et al. 2000). Factors beyond seed distribution in relation to disturbance and myrmecochory are unknown, but findings by Fyles (1989) and Leckie et al. (2000) imply *C. sempervirens* maintains remnant populations of dormant seeds. Within these parameters, the distribution of above-ground plants, combined with complexities associated with predictors of the spatial and temporal distribution of dormant seeds, make *C. sempervirens* a suitable species to examine from a metapopulation perspective.

Biotic factors related to dispersal may contribute to non-random, clumped seed bank distribution. These clumped seed patterns are often mediated by habitat-specific animal dispersers that direct seeds to areas where conditions are favorable for survival and/or germination (Howe & Smallwood 1982; Husband & Barrett 1996; Purves & Dushoff 2005). Watt (1947) identified seed dispersers' habits as an important factor in determining seed distribution and the ability for subsequent seedling establishment.

Ants transport seeds of myrmecochorous species to nests to feed on eliaosomes. Eliaosomes are lipid-rich deposits found on seeds and provide a source of nutrition for adult ants, or more often, ant larvae. In a review of myrmecochory Gómez and Espadaler (1998) reported mean dispersal distance of myrmecochorous seeds by ants was 0.96-m, but farther distances have been reported (Alba-Lynn & Henk 2010; Cain et al. 1998). Because ant nests are located under rocks or within stumps and logs, seeds of myrmecochorous species often escape detection by seed predators (Alba-Lynn & Henk 2010; Heithaus 1981). Seeds transported into nests deep within the soil or within cracks in rocky substrate could also benefit from increased protection from intense fire heat (Hanzawa et al. 1988).

Seed dispersal mediated by mammals and birds results in even greater dispersal distances away from source plants (Chambers & MacMahon 1994; Rogers & Applegate 1983; Stiles 1980). Other mechanisms, including secondary dispersal by wind and water, may increase the distance seeds are dispersed from parent plants and further complicate seed distribution patterns (Egawa & Tsuyuzaki 2013; Shimono et al. 2006; Vander Wall et al. 2005).

The benefits of long-distance seed dispersal depend on landscape characteristics as well as patch area and subpopulation size (Dostál & Pugnaire 2005). Although long-distance dispersal may increase the probability of connectivity between suitable habitat patches, this advantage is not evident in landscapes where suitable habitat has a clumped distribution. Aggregation of suitable habitat patches increases the probability that seeds will be lost within the unsuitable habitat matrix (Johst et al. 2002).

Gaps created by fire represent newly opened habitat suitable for germination of early-successional species and influence seed bank formation and above-ground vegetation distribution (Ahlgren 1960; Turner et al. 1997). Because fire occurrence is often stochastic and suitable habitat conditions ephemeral, long-term seed dormancy strategies are advantageous for early-successional plants (Leckie et al. 2000; Marks 1974; Olano et al. 2002; Venable & Brown 1988). In fire-prone habitats, natural fire regimes clear understory and canopy vegetation creating suitable light conditions for germination, or fire may induce germination of seeds requiring intense heat to break seed coats (Ahlgren & Ahlgren 1960; Baskin & Baskin 1998). Population-level benefits of fire in relation to the seed bank are well-described (see Ayre et al. 2006; Dolan et al. 2008; Uchiyama et al. 2006). Factors that influence the fate of post-disturbance seed banks are less well-understood. As successional processes change habitat conditions, remnant seed populations may become isolated within a greater unsuitable habitat matrix, or could potentially be connected to plant subpopulations in suitable habitat by active seed dispersal or future disturbance.

In addition to biotic and disturbance-related factors, the distribution of seeds varies spatially and temporally depending on habitat-specific influences (Parker et al. 1989, Pickett & McDonnell 1989). Factors specific to landscape and persistent, plant subpopulations include distance of seeds to source individuals, successional stage, topography, and soil characteristics (Ashton et al. 1998; Beatty 1991; Parker et al. 1989, Pickett & McDonnell 1989; Putz 1983). Litter accumulation as a result of successional processes has been shown to decrease seed emigration and increase seed retention (Egawa & Tsuyuzaki 2013). Soil depth, vertical movement, and moisture levels influence seed bank structure, dormancy time, and germination rates (Benvenuti 2007; Benvenuti et al. 2001; Bonis & Lepart 1994).

The objectives of this study were to (1) examine how the distribution of the seed bank of the early-succession species *C. sempervirens* varies spatially and temporally in relation to landscape heterogeneity and (2) uncover how factors influencing seed distribution ultimately influence above-ground subpopulation persistence. The question addressed in this study was: how does primary dispersal by ants combined with landscape factors and past fire occurrence influence the distribution of *C. sempervirens* seeds? I addressed this question with the following hypotheses and predictions (Fig. 1):

- Primary seed dispersal by ants should create a seed bank within suitable habitat on rock outcrops and a restricted "shadow" in the forest immediately surrounding the rock outcrops. If input into this shadow is relatively continuous and not dependent on fire, this shadow should be more enriched in *C. sempervirens* seeds than soil in other parts of the forest matrix.
- The abundance of *C. sempervirens* in the seed bank on rock outcrops and in the adjacent forest "shadow" is related to the physical size/area of the rock outcrop and/or the current *C. sempervirens* plant density. If rock outcrop habitat is suitable for more above-ground *C. sempervirens* plants, then the seed bank will be more enriched in the immediate surroundings.
- If past fires influence the distribution of seeds, I expected seeds to be present at greater distances from rock outcrops into the surrounding forest matrix. Patterns would likely reflect both spatial and temporal characteristics of the fire history and seed bank longevity.
- Landscape features (topography, soil depth, and land cover types) influence secondary dispersal mechanisms as well as seed retention and viability. I expected seeds to be found

at greater distances into the forest matrix in relation to topography and also expected seed presence to be greatest in areas more hospitable for seed bank persistence.

METHODS

Study area

The 4512-ha study area is located near the south shore of Lake Superior, 11-15 km northwest of the city of Marquette in Michigan's Upper Peninsula (Fig. 2). Physical features of the study area include uplands with Archean granite-gneiss outcrops, wet upland depressions, streams, and ponds. Soils in much of the study area are classified as well-drained spodosols. Elevation ranges from 184-372 m.

In total, the area contains 338 rock outcrop areas with open canopy conditions suitable for above-ground *C. sempervirens*. The rock outcrop area ranges from 30-13,461 m^2 with distances between outcrops ranging 10-412 m. Outcrop seed banks and above-ground *C. sempervirens* plants are commonly found in areas with shallow soil accumulation such as crevices formed by freeze-thaw action, small depressions, or mats dominated by moss, fruticose lichens, and xerophytic vegetation (e.g. *Arctostaphylos uva-ursi*, *Vaccinium angustifolium*, *Gaylussacia baccata*, and *Danthonia spicata*).

Approximately 80% of the landscape surrounding outcrops is classified as northern hardwood or hardwood-conifer forest, dominated by aspen (*Populus* spp.), white birch (*Betula papyrifera*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), balsam fir (*Abies balsamea*), and scattered stands of mixed pine (*Pinus resinosa, P. strobus, P. banksiana*). Eight post-fire stands (<10-ha) ranging in age from 3-76 years were identified within the study area (Fig. 1). The rest of the study area was dated by examining increment cores from canopy trees and determined to be dominated by 85- to 120- year-old second growth forest, with a mixture of older remnant pine and hemlock (*Tsuga canadensis*).

The climate is highly modified by Lake Superior and characterized by cold, snowy winters and warm summer. The mean monthly temperature range from a maximum of 24.6° C in July to a low of -5.4° C in January. Temperature extremes range from a minimum of -35° C to a maximum of 37° C. Mean precipitation for the area is 90.5-cm with 52% occurring April - September. Mean snowfall for the area is 518.2-cm. The mean annual growing season is 75 days.

Site selection and sampling design

Outcrops and the approximate boundaries of the eight burn sites were digitized using ESRI ArcMap 10.0 software. The boundaries of recent burns (≤ 6 years) were visually estimated in the field. The boundaries and approximate years of fire occurrence for burn sites > 6 years were field-checked by collecting increment cores near the base of >10 (depending on burn area) aspen, paper birch, and/or jack pine, which were most likely to establish within a few years of the fire. I also collected increment cores from any remnant pines found within burn areas to examine any sudden growth "releases" following canopy-altering fire. Fire years were estimated from the maximum ages of post-fire trees, and refined to an exact year based on release dates.

A total of 324 random seed bank sampling points were generated in upland habitat in the closed forest matrix. Points were located 0-1269 m from rock outcrops and were located at least 10 m apart. Because the post-fire stands were fairly small and inadequately covered by the initial sampling design, I sampled 15-30 additional random points within each of these burns for a total of 165 seed bank sampling points. The number of points sampled within each burn depended on the area of the fire. These samples were used to examine trends in seed bank abundance with increasing stand age.

Rock outcrops were sampled separately from the forest matrix. I randomly sampled 144 of the 338 outcrops to estimate the abundance of flowering and rosette *C. sempervirens.*

Samples from the seed bank were also taken from 28 of the 144 outcrop sites. These samples were used to see whether persistent seed banks form on rock outcrops, and, if so, what factors influence the abundance of *C. sempervirens* seed.

Sampling procedures

Forest matrix seed bank

The general approach for collecting and processing seed bank samples followed Mladenoff (1990). The soil core dimensions were 5-cm in diameter by 10-cm deep. Eight cores were collected in each of the cardinal and sub-cardinal directions, 1-m from each sample point. Average litter and soil depth was calculated from 8 measurements taken adjacent to core locations. Litter was compacted by a 22-g washer and measured from top to soil surface. Soil depth was operationally defined as the depth a 6-mm diameter steel rod could be pushed into the soil before encountering rock.

The viable *C. sempervirens* seed bank was assessed by seedling emergence. The 8 samples from each random point were pooled for a total soil volume of roughly 2.75 liters. This soil was spread into plastic trays and covered with a light layer of sphagnum moss (Mladenoff 1990). Trays were watered every 12 hours and kept in a greenhouse with a 12-hour light/12-hour dark cycle. Approximate daytime temperature was 29°C and nighttime temperatures ranged from 10 - 18°C. Six control trays of a sphagnum and sterilized soil mixture were also placed in the greenhouse to detect any contamination. Initial trials indicated *C. sempervirens* seeds germinated within 5-14 days after placement in the greenhouse. Based on this observation, any un-germinated areas of the trays were stirred after 21 days. The total number of *C. sempervirens* seedlings were identified and counted for each tray after 35 days.

Above-ground subpopulations and outcrop seed bank

C. sempervirens plants on outcrops were sampled from July through September, 2013. The coordinates of each sampling point served as the center of a 10-m radius plot. Within each plot, I counted the total number of flowering and rosette *C. sempervirens* plants. I also counted the total number of seed pods for plants that had gone to seed. The percent-cover of bare rock and groundcover (vegetative, litter, and bare soil) was visually estimated. Seed bank samples were also taken at 28 outcrops. The coordinates of each outcrop point served as the center of a 2-m radius sampling plot. Because soil is was limited on outcrops, soil seed bank samples were collected by filling eight soil cores from any sources of soil in rock cracks, crevices, and shallow depressions within 2-m of the sampling point.

Landscape and physiographic data

Values for addition variables were extracted from GIS layers for each sampling point (Table 1). The area (ha) of each rock outcrop and the distance (m) to nearest outcrop for seed bank sample points were determined using ESRI ArcMap 10.0 software. Land cover variables were extracted from a 2001 Upper Peninsula Land Cover IFMAP/GAP map (30-m resolution). The original data set containing 30 classes was reclassified to include five classes: conifer, hardwood, hardwood/conifer, herbaceous, and non-vegetative. Soil orders and drainage classes were imported from the Marquette County 2000 SSURGO soil maps.

Physiographic variables, including elevation, slope, and aspect, were derived from a 10-m DEM. GIS layers for hillshade, flow accumulation, and curvature were also extracted from the DEM and used to construct a modified version of the Iverson et al. (1997) integrated moisture index (IMI). The IMI was used as an indicator of moisture accumulation. Moisture accumulation is considered to be higher in areas with minimal solar accumulation (hillshade), low slopes (flow accumulation), or in depressions (curvature) (Iverson et al. 1997). Hillshade, flow accumulation, and curvature accounted for 50%, 35%, and 15% of the IMI, respectively (Yost 2008).

Outcrop and land-cover layers were converted to ASCII format and imported into FRAGSTATS (version 4.0, www.umass.edu/landeco/research/fragstats/fragstats.html) to extract several landscape metrics. Moving window analysis was applied to the percentage of landscape in rock outcrop at a scale of 100-m radius. In this procedure, the percentage of landscape in rock outcrop is calculated for a 100-m radius window that moves one pixel at a time across the entire study area, providing a continuous map of the outcrop "neighborhood." This variable was used to test whether the presence of more or larger outcrops in an area might be a better predictor of seed bank abundance than simply distance to the nearest outcrop. Results from moving window analyses and all other GIS-derived variables were tabulated for each sample point.

Data analysis

Traditional regression models assume linear or simple non-linear response, but these models are often unrealistic for modeling response to environmental gradients. Based on these limitations, I used nonparametric multiplicative regression (NPMR) in HyperNiche (version 2.0, MjM Software, Gleneden Beach, OR, US) to allow for the possibility of nonlinear relationships between response and predictor variables. NPMR uses a smoothing function with leave-one-out cross validation to estimate response variables (Berryman & McCune 2006). Both binary and quantitative models were constructed using a local mean estimator with Gaussian weighting of seed and above-ground plant response in relation to predictor variables. Binary model quality was assessed by log likelihood ratio (log*B*) which expresses model improvement over a naive model. A log*B* > 0 indicates the fitted model is better than the naive model while a negative log*B* indicates cross-validated estimates from the fitted model are worse than the naive model (Binder

& Ellis 2008). Quantitative models were assessed by a cross-validated R^2 (xR^2) The xR^2 excludes each data point from the basis for the estimate of the response at that point, so in the event the model is weak, the xR^2 is negative (Berryman & McCune 2006). NPMR does not fit coefficients in a fixed equation. Instead NPMR fits tolerances used in the Gaussian smoothers (Berryman & McCune 2006). A scree plot of xR^2 or log$B$ versus the number of variables was used to select the final model. Significance of models was evaluated by Monte Carlo permutation tests which compared the estimated response variable to an average estimation calculated by 100 random permutations among the data set.

Time since fire was only reliably determined for a few small stands. Although these stands were targeted for additional sampling of their seed banks, I analyzed trends in seed bank abundance in relation to fires separately using non-parametric correlation analysis. In addition to NPMR analysis, I also further examined seed bank abundance in relation to nearest above-ground subpopulation variables using non-parametric correlation analysis. Mean seedling abundance from forest seed bank samples was compared to mean outcrop seedling abundance using a Mann-Whitney U independent-samples test (IBM SPSS Statistics, version 21).

RESULTS

C. sempervirens seeds were present in 111 of the 517 seed bank samples: 90 samples had 1-10 seedlings present, 19 contained 11-30 seedlings, and 2 samples had >30 seedlings. 14.0% (n = 324) of forest seed bank samples contained *C. sempervirens* seedlings compared to 39.2% (n = 28) of outcrop seed bank samples. The outcrop seed bank had a mean abundance of 6.2 (± 3) seedlings, which was significantly greater than the mean abundance of *C. sempervirens* seedlings from forest seed bank samples (1.1 ±0.3) (U =3.25; n_1=324, n_2=28; p= 0.001).

Of the 144 outcrops sampled, 94 contained *C. sempervirens* plants within sample plot boundaries. *C. sempervirens* had a mean density of 0.04 (±0.006) plants/m^2 on outcrops, with 86.6% of plants in flower and the rest in vegetative rosettes (Table 2).

Forest seed bank spatial and temporal patterns across the landscape

A nonparametric regression model based on the binary response of seed presence or absence in relation to landscape and physiographic predictors was selected from a stepwise free search. The model indicated distance from nearest rock outcrop and elevation best explained the presence of *C. sempervirens* seeds within the forest matrix (log$B$ = 11.9, p = 0.01) (Table 3).

The probability of finding *C. sempervirens* in the seed bank declined exponentially with distance from rock outcrop (Fig. 3). Although the model predicted a slight probability of finding *C. sempervirens* in the seed bank beyond 200 m, the actual maximum distance detected was 175-m from the outcrop. No seedlings were detected at distances 176 - 1269 m from nearest outcrop. I isolated just the first 70-m from rock outcrops in a model to improve the resolution of trends immediately surrounding the outcrops. Highest seed abundance occurred in the 0-20 m range, (Fig. 3 inset), while seed presence was greatest up to 40-m from outcrops. Although seeds were more commonly found up to 40-m, seedling abundance in the 0 to 40-m forest buffer shared only a modest positive correlation with plant abundance on the nearest rock outcrop ($r = 0.215$, $p = 0.016$, $n = 111$) and nearest outcrop area ($r = 0.205$, $p = 0.021$, $n = 111$).

The probability of finding *C. sempervirens* in the seed bank also increased steeply with elevation (Fig. 4). Areas within the forest matrix that surround expansive rock outcrop complexes—most located at elevations > 300 m—had the highest probability of seed occurrence.

Trends in seedling abundance with time since fire were highly variable, but several of the most recent fire sites clearly had seed banks enriched with *C. sempervirens* (Fig. 5). Seed abundance in the forest seed bank shared a negative correlation with stand age ($r = -0.409$, $p < 0.001$, $n = 165$). Although *C. sempervirens* was not detected in the 76-year old burn site, *C. sempervirens* was present in 20% of the plots in the older forest matrix, which was predominantly 80 to 120-year-old hardwoods.

Outcrop plant populations and their seed banks

The presence of *C. sempervirens* in the seed bank within rock outcrops was also modelled as a function of rock outcrop size, density of *C. sempervirens* plants, groundcover predictors, and various landscape physiographic variables (Table 1). The only variable identified in the outcrop seed bank model was the percentage of vegetative groundcover ($\log B = 1.4$, $p = 0.01$) (Fig. 6). The likelihood of finding *C. sempervirens* in the seed bank increased when the percentage of total groundcover exceeded 60% (Fig. 7). The abundance of viable seeds within the outcrop seed bank shared no significant relationship with plant density ($r = -0.149$, $p = 0.402$, $n = 28$). Indeed, seeds were present in the absence of above-ground plants, while sites with large plant subpopulations often displayed no discernable *C. sempervirens* seed bank.

Similar to the seed bank model, percentage of groundcover was the best variable that explained plant presence-absence ($\log B = 5.0$, $p = 0.01$) (Fig. 8) and plant abundance ($xR^2 = 0.07$, $p = 0.02$), although the association was weak in both models. Unlike the seed bank, which had an optimum at >60% groundcover, probability of plant occurrence peaked at 10-30% groundcover, declining thereafter. Likewise, plant abundance peaked at intermediate levels of groundcover, with an optimum of 6-50% (Fig. 9).

DISCUSSION

Plant and seed bank dynamics on rock outcrops

Both plant abundance and seed bank occurrence on rock outcrops were best explained by the patchiness of the groundcover. Not surprisingly, plants were most abundant at intermediate levels of groundcover, which describes the small islands of soil and lichen accumulation where *C. sempervirens* is often found. In contrast to above-ground plants, seed banks were more enriched in areas of higher groundcover. These areas form islands within the rock outcrop, and the more developed ones support scrubby *Pinus banksiana* and dense patches of *Vaccinium* spp., *Danthonia spicata*, *Diervilla lonicera*, and *Arctostaphylos uva-ursi.* One explanation for the enhanced seed bank within these islands is that vegetation traps seeds and decreases the potential for primary or secondary dispersal events (Egawa & Tsuyuzaki 2013; Houle 1990). *C. sempervirens* seeds are shade-intolerant and germination is triggered by exposure to direct sun or soil warming. As long as patches remain open to high light intensity the trapped *C. sempervirens* seeds will germinate and ultimately lead more above-ground plants at these locations. If groundcover continues to increase, above-ground plants will be outcompeted and any remaining seeds contribute to the formation of the persistent seed bank.

Surprisingly, the presence and abundance of seed-bearing *C. sempervirens* plants did not dictate patterns in the outcrop seed bank. I assumed that there might be almost continual renewal of new plants in outcrop edge habitats since the shallow soils and high sunlight conditions appear ideal for immediate germination; indeed, it seems plausible that persistent seed banks might only play a modest role in rock outcrop subpopulation dynamics. However, I found that above-ground *C. sempervirens* plants were fairly uncommon on rock outcrops; some outcrops totally lacked plants even though a persistent seed bank was present, suggesting that opportunities for seed germination occur sporadically. In edge habitat and smaller groundcover patches ideal for above-ground *C. sempervirens* plants, seeds may also be easily lost—washed or blown away or dispersed by ants into rock cracks and/or more densely vegetated islands. In this study, I observed ants transporting seeds from parent plants to nearby cracks in rock. Sporadic seed germination may follow frost heaving or erosion events that dislodge buried seeds. The formation of persistent seed banks on rock outcrops suggests that extinction events for plants on outcrops may be short-lived.

Forest seed bank dynamics: reconciling the roles of dispersal vectors and fire

Dispersal into the forest matrix

The *C. sempervirens* forest seed bank was not random or uniform; rather it was related to time since last fire, proximity to persistent source populations on rock outcrops, and elevation. Limited seed dispersal into the greater forest matrix and long intervals between large, stand-altering fires hint that seed bank patterns away from rock outcrops in the greater forest matrix may develop somewhat predictably over very long time periods.

Seeds within the forest seed bank were found in greater abundance within close proximity to outcrops and potential parent plants. The enrichment of the seed bank in the immediate surroundings of a rock outcrop is consistent with highly localized ant dispersal. Studies by Andersen (1988) and others (Hughes & Westoby 1992; Willson 1993; Alba-Lynn & Henk 2010; Gómez & Espadaler 1998) indicate most ant-dispersed seeds are found in close proximity to source plants. Typical mean dispersal distances are 2-m or less from parent plants (Alba-Lynn & Henk 2010; Gómez & Espadaler 1998), but observations of dispersal of seeds to distances greater than 10-m have been reported for other myrmecochorous species (Andersen 1988).

Seeds dispersed within close proximity to parent plants may have increased probability for further secondary seed dispersal (Denham et al. 2009; Lamont et al. 1993). Seeds originally landing in/transported to exposed rock areas that lack physical barriers, such as soil or litter, are exposed to rainfall, wind, or water from snow thaw. These factors are well-known secondary dispersal mechanisms (Egawa & Tsuyuzaki 2013). Many of the rock outcrops in the study area have smooth, steep sides that likely facilitate secondary dispersal into the nearby forest matrix.

The distribution of seeds in relation to distance from potential parent plants partially supports the ant dispersal hypothesis, but does not explain the presence of seeds within the greater forest matrix. Although presence of seeds generally decreased with increased distance from outcrops, *C. sempervirens* seeds were found up to 175-m from potential source populations indicating that factors beyond myrmecochory explain seed presence.

Another potential dispersal vector of *C. sempervirens* is the snowshoe hare (*Lepus americanus*), which has not been previously reported. I observed hare herbivory of *C. sempervirens*, including tops that probably had seed pods, at many rock outcrops in the study area. Hares are a potential endozoochorus species. Izhaki and Ne'eman (1997) found 43% of randomly collected hare pellets contained viable *Retama raetam* seeds, and they proposed that hares might be an important long-distance disperser (see also Cosyns et al. 2005). Small seeds, similar to those of *C. sempervirens*, are most likely to remain viable in hare pellets (Pakeman et al. 1999). An examination of the viability of *C. sempervirens* seeds after digestion by hares is needed to understand the influence of endozoochory on the distribution of seeds across the landscape.

Any long-distance dispersal event would tend to blur the effects of source populations. A good example of this is *Aralia hispida,* a seed bank species that also forms persistent populations on rock outcrops but also emerges en masse after fires in forest habitat (Pratt 2003). Pratt (2003) found that the distribution of forest seed bank was unrelated to distance from source populations on outcrops and attributed the widespread occurrence of *Aralia hispida* to primary seed dispersal by mammals, which included black bears (*Ursus americanus*) and foxes (*Vulpes vulpes*, *Urocyon cinereoargenteus*).

Seed distribution in relation to landscape

Landscape features and soil characteristics are known to influence seed bank patterns. Elevation was an important predictor of seed bank presence in my study area. One explanation for this trend is larger source populations that thrive on granite knobs and exposed ridges. These areas are dominated by scrubby, xerophytic vegetation and pines and probably have increased susceptibility to lighting-induced fire (Albert 1995). Frelich and Lorimer (1991) reported 11 lighting-induced fires occurred during the extremely dry summer of 1976 in the Porcupine Mountains region of Michigan's Upper Peninsula. Similar to many of the burn sites within my study area, most of these fires were small and did not reach the canopy, but instead, smoldered in the duff layer (Frelich & Lorimer 1991). In my study area, large expanses of rock with intermittent areas of shallow soil and litter prevent deep root penetration and could allow ground or surface fires to affect canopy vegetation. Based on these scenarios, small, lighting-induced fires would not only increase suitable habitat conditions for above-ground *C. sempervirens* but would also lead to continual inputs into the surrounding seed bank.

In addition to increased rock habitat for above-ground plants, the shallow, dry, well-sorted soils in these areas most likely increase the probability that seeds will remain viable over long time periods. Moore and Wein (1977) demonstrated that density of the viable seed bank decreased in wet, lowland sites. Seeds dispersed to lower elevations areas may encounter deeper, more hydric soils. These seeds may not receive appropriate germination cues or may be susceptible to factors that increase seed mortality (Augspurger & Kelly 1984; Schafer & Kotanen 2003). The increased presence of *C. sempervirens* seeds at higher elevations does not necessarily imply that seeds are not dispersed to low-lying areas. The absence of seeds in these areas may actually represent inhospitable conditions that decrease seed viability.

Seed bank creep model

Observations of *C. sempervirens* seed abundance the local seed bank extends ≤ 20 m from outcrops for this species. In the event of a stand-altering fire encompassing outcrop habitat, the open-canopy conditions would induce germination of seedlings from this near-outcrop seed bank. The seeds produced from these plants would allow the seed bank to expand, or creep, ≤ 20-m further away from the original local seed bank. In the event of successive fires, the creeping seed bank could encompass outlying seeds dispersed a greater distances by wind, water, or zoochory. Eventually, depending on the size and return interval of fires, the creeping seed bank could affect outcrop subpopulation dynamics by temporarily linking patches or creating overlapping seed shadows.

The viability of the seed bank creep model (Fig. 10) is dependent upon seed bank longevity being greater than the fire return interval. Similar to Fyles (1989), I demonstrated that seed banks of this species persist for >80 years, but an upper limit could not be determined in this study. Historic intervals for stand-replacing fires in the mixed-pine/hardwood forests of the Upper Great Lakes Region range from 250-400 years (Cleland et al. 2004; Stearns 1949). Frelich and Lorimer (1991), however, calculated that disturbances, including surface and light to medium intensity canopy fire, have a return interval of 52-119 years in Michigan's Upper Peninsula. These more-frequent disturbances may work in connection with larger, less-frequent fires to induce seed bank creep into the forest matrix. If disturbance induces the seed bank to creep in 20-m increments into the forest matrix, and small, localized fires occur, on average, every 86 years, it would take approximately 9 successive fires, or approximately 725 years for seed to be present 175-m from the original outcrops. In this time, the creeping seed bank would also encompass outlying seeds dispersed by wind, water, or zoochory and maintain the presence of seeds in the forest matrix.

SUMMARY AND CONCLUSIONS

This study provided much needed insight into the mechanisms influencing seed bank formation and distribution and above-ground subpopulation persistence for an early-succession species within a variable landscape. Results from NPMR models indicated both seed and above-ground plant distribution are not random but rely upon spatial and temporal predictors. Increased seed presence in relation to plant habitat demonstrated the forest seed bank distribution has depends strongly on distance to source populations and primary dispersal activity, but the presence of seeds within the greater forest matrix also indicates reliance on landscape, physiographic, or disturbance-related factors. Dissimilar to the forest seed bank, the formation and persistence of a *C. sempervirens* seed bank, along with above-ground subpopulation persistence, on outcrops was best explained by temporal predictors associated with successional processes. Depending on seed bank longevity and the fire return interval, primary and secondary dispersal mechanisms influencing forest seed bank distribution may also influence subpopulation persistence as outlined in the seed bank creep model. Results from this study could lead to better predictions of the distribution of the dormant seed bank for other early-succession species and also provide an understanding of how this distribution, along with other habitat-specific parameters, have the potential to influence plant metapopulation dynamics at a landscape scale. The approach used in this study signifies the importance of incorporating spatial and temporal aspects of seed distribution in future population studies within a metapopulation framework.

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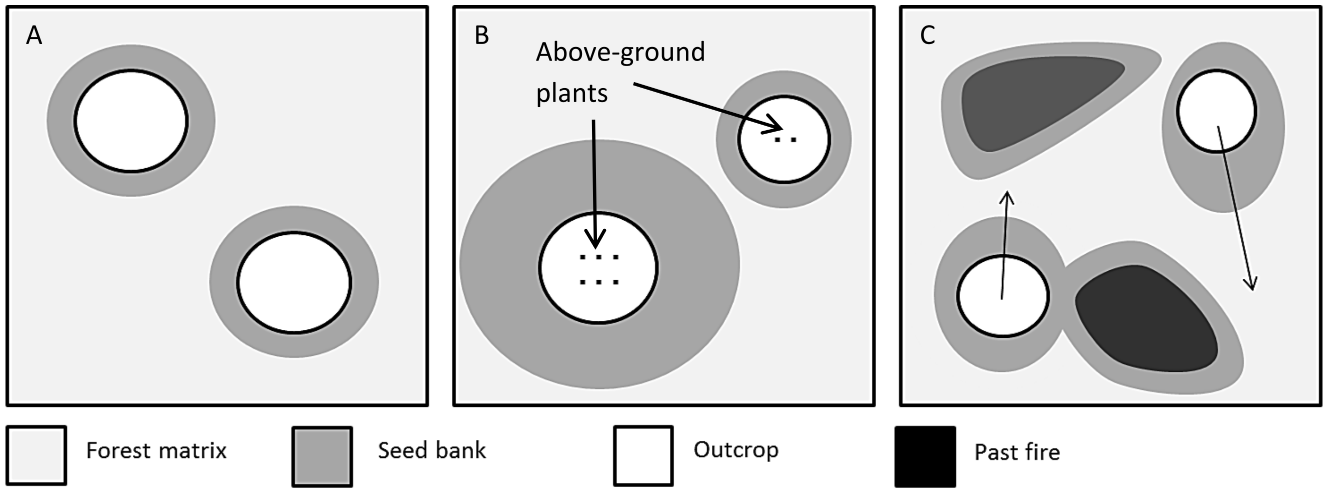


Fig. 1. Hypotheses and predictions for the distribution of *C. sempervirens* seed bank. A) Seed distribution based solely on localized ant dispersal would create a seed bank on rock outcrops and a restricted shadow in the forest immediately surrounding the rock outcrops. If input into this shadow is relatively continuous, this shadow should be more enriched in *C. sempervirens* seeds than soil in other parts of the forest matrix. B) If rock outcrop habitat is larger and more suitable for more above-ground *C. sempervirens* plants, then I expected a more enriched seed bank would be in the immediate surroundings of the outcrop and also farther into the forest matrix. C) If past fires influence the distribution of seeds, we expected seeds to be present at greater distances into the surrounding forest matrix. Patterns would reflect fire history, seed bank longevity, dispersal after recurrent fires. We also expected secondary dispersal mechanisms to be influenced by landscape features. The presence of seeds would also be related to suitable habitat conditions that favor seed viability.

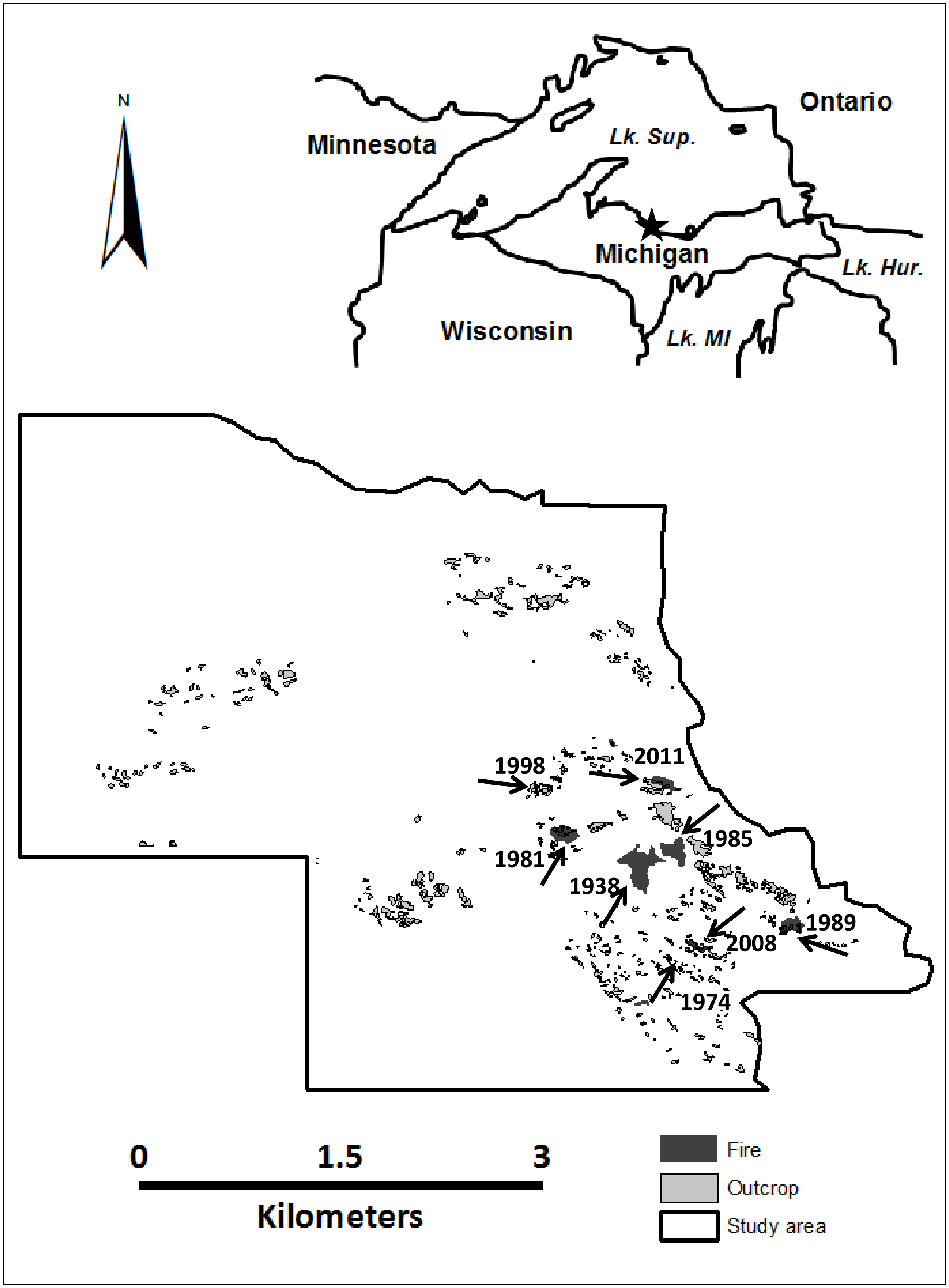


Fig.2. Map of study area located approximately 15 km north of Marquette, MI. Outcrop locations and fire sites with approximate year of fire are indicated within the figure.

Table 1. Descriptions of predictor variables used in binary and quantitative forest seed bank (FSB), outcrop seed bank (OSB), and above-ground plant (AGP) nonparametric multiplicative regression models.

Predictor variable	**Classification**	**Description**	**Model/s**
Litter depth	quantitative (cm)	Measured from surface to bare soil after compacting litter with a 22 g washer	FSB
Soil depth	quantitative (m)	Measured from bare soil layer to bedrock	FSB
Distance	quantitative (m)	Distance to nearest rock outcrop	FSB; OSB; AGP
Integrated moisture index		Derived from hillshade, flow accumulation, and curvature from 10 m digital elevation model (DEM) (Iverson et al. 1997; Yost 2008)	FSB; OSB; AGP
Slope	quantitative (°)	From 10 m digital elevation model DEM	FSB; OSB; AGP
Aspect	quantitative	From 10 m DEM, transformed to a linear measure of "southwestness" using a modified Beers transformation (Beers et al. 1966, Hooten 2001): SWST = cos(A +135*π/180)	FSB; OSB; AGP
Elevation	quantitative (m)	From 10 m digital elevation model (DEM)	FSB; OSB; AGP
Percentage of landscape	quantitative (%)	From moving window analysis (100 m) for land cover classes: rock, conifer, hardwood, hardwood/conifer, herbaceous, no vegetation	FSB; OSB
Percent groundcover	quantitative (%)	Total percent groundcover within plot, visually estimated at each plot	OSB; AGP
Above-ground plants	quantitative	Total number of *C. sempervirens* present within each rock outcrop plot	OSB
Seed pods	quantitative	Total number of *C. sempervirens* seed pods present within each rock outcrop plot	OSB

Table 2. Seed bank and outcrop descriptive statistics. Mean (std) and median area and distance to nearest neighbor for all rock outcrops located within the study area (*n* = 338). Mean (std) and median number of flowering and rosette *C. sempervirens*, mean (std) and median number seed pods, and above-ground plant percentages represent rock outcrop sampling locations (*n* = 144). Percentage of rock outcrops with a persistent seed bank represent outcrop seed bank sampling locations (*n* = 28). Forest seed bank statistics represent sampling locations (*n* = 324).

	n	**Mean (std)**	**Median**
Forest seed bank seedling abundance	324	2.3 (0.4)	0
Outcrop seed bank seedling abundance	28	6.2 (3.0)	0
Outcrop area (m^2)	338	1173 (179)	428
Outcrop nearest neighbor (m)	338	64.6 (37.8)	56.6
Flowering *C. sempervirens* per outcrop	144	12.0 (1.6)	4
C. sempervirens rosettes per outcrop	144	1.9 (0.3)	0
Seed pods per flowering plant	144	10.5 (1.0)	8.5
% of outcrops with above-ground *C. sempervirens*	144	65.3	
% of outcrop seed bank samples with *C. sempervirens*	28	39.2	
% of forest seed bank samples with *C. sempervirens*	324	20.0	

Table 3. Nonparametric multiplicative regression models indicated distance from outcrop, elevation, and percent groundcover predict the presence of the forest seed bank (n = 324) (log$B$ = 11.9) and rock outcrop seed bank (n = 28) (log$B$ = 1.4) and plant subpopulation (n = 144) presence (log$B$ = 5.0) and abundance (xR^2 = 0.07).

Model	***n***	**Response variable**	**Predictor variable/s**	**Model fit**	**Tolerance**	**Sensitivity**	***p***
Forest seed bank	324	Seedlings (binary)	distance from outcrop	log$B$=11.9	67.6	1.1	0.01
			elevation		13.2	0.6	
Outcrop seed bank	28	Seedlings (binary)	% ground-cover	log$B$=1.4	7.5	2.0	0.01
Above-ground plants	144	Plants (binary)	% ground-cover	log$B$=5.0	8.5	1.1	0.01
Above-ground plants	144	Plants (quantitative)	% ground-cover	xR^2=0.07	8.5	1.3	0.02

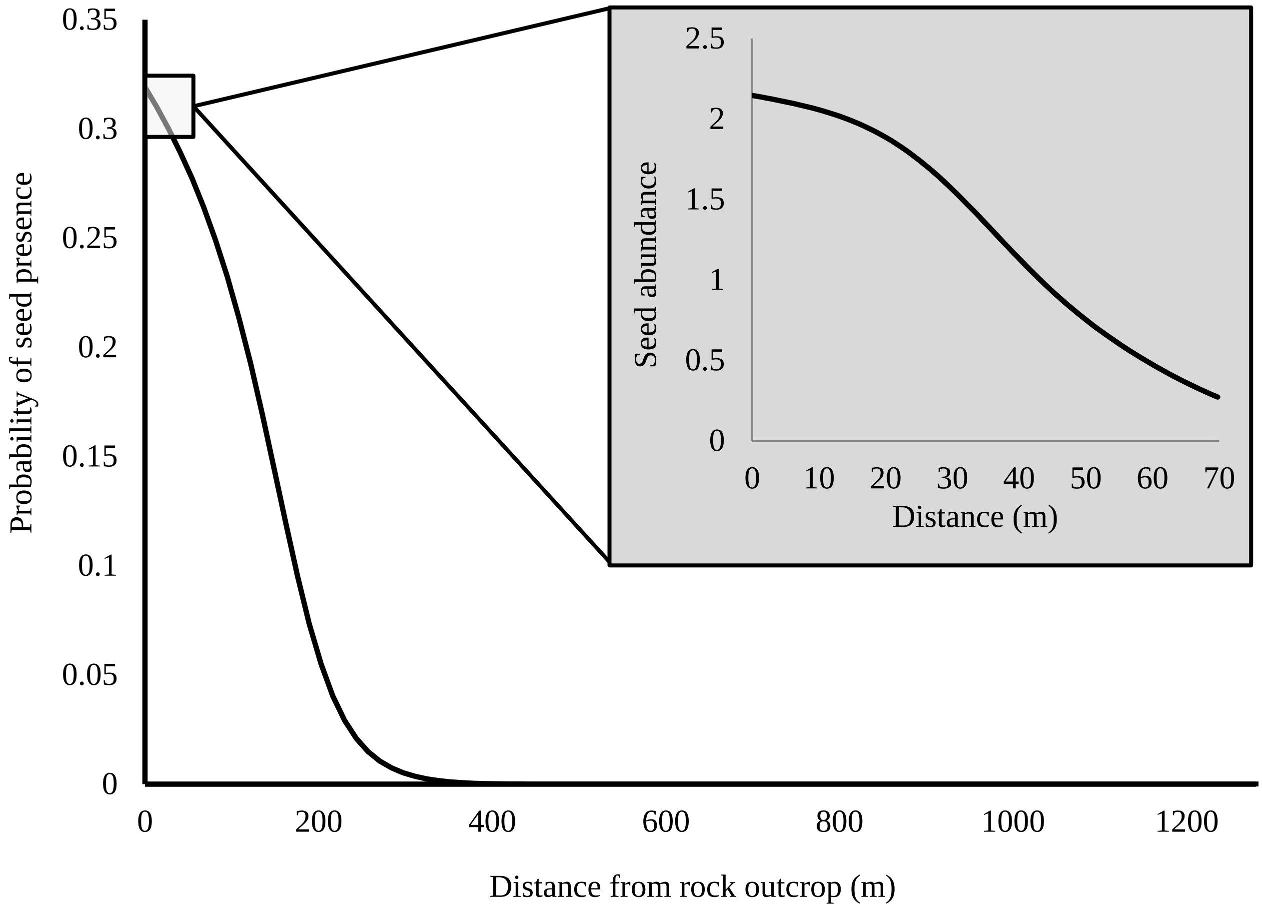


Fig. 3. Probability of seed presence in the forest seed bank in relation to distance (m) from nearest outcrop using nonparametric multiplicative regression in HyperNiche 2.0 (n = 324). Insert depicts probability of seed presence in relation to distance up to 70-m from outcrops. The probability and abundance curves were generated from a scatterplot using a locally weighted mean. The abundance curve was generated after removing one outlier (63 seedlings) occurring 20-m from a rock outcrop.

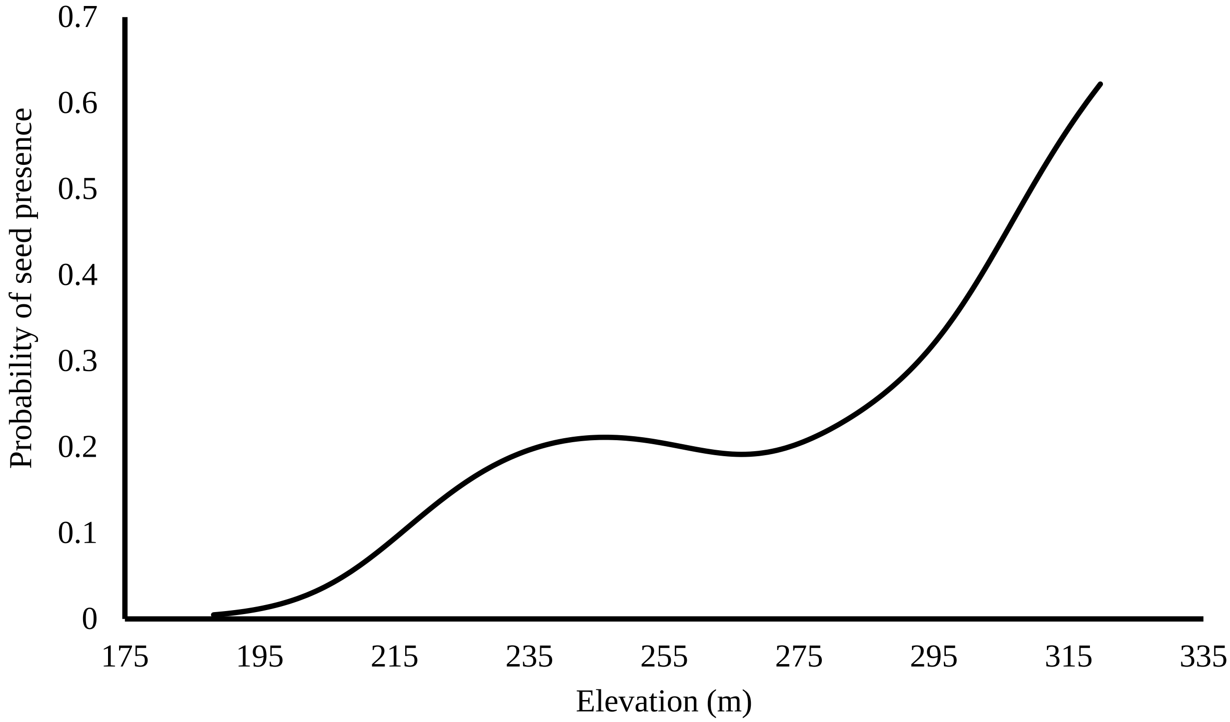


Fig. 4. Probability of seed presence in the forest seed bank in response to elevation (m) using nonparametric multiplicative regression in HyperNiche 2.0 (n = 324). The smoothed curve was generated from a scatterplot using a locally weighted mean. The lowest elevation sampled within the study area was 188-m.

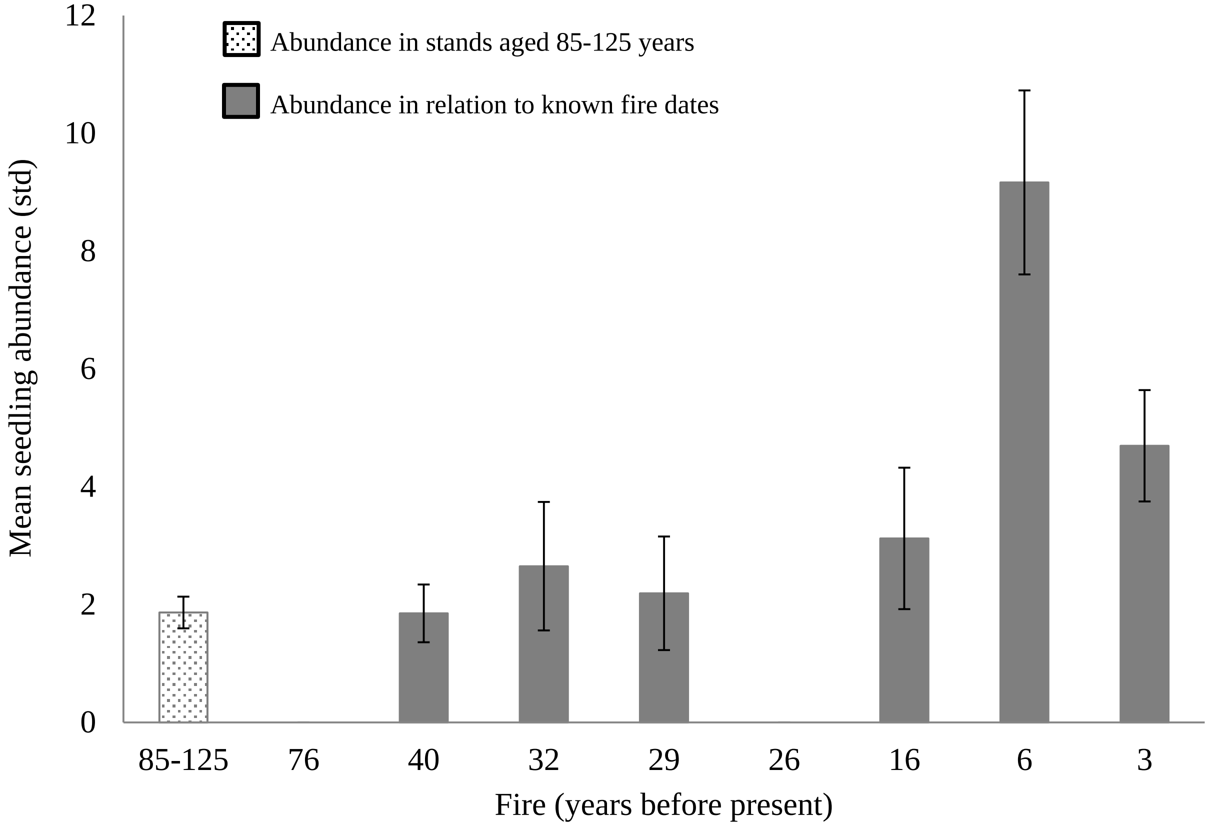


Fig. 5. *C. sempervirens* mean seedling abundance in relation to years-before-present since past fire within the study area (*n* = 165). Depending on the area of the burn, each fire site contained 15-30 sampling points located at least 10-m apart. The reference column () represents mean seedling abundance in the surrounding greater forest matrix (*n* = 324). Years-before-present since past fire in these areas range 85-125 years. Seedling abundance was determined by seedling emergence from 2.75 liters of soil collected at each sampling location. The frequency of seedling occurrence (proportion of samples with seedlings) ranged from 0-77% for the 3-76 year-old fire sites and 15% for samples from 85-125 year-old stands. Frequencies were proportional to mean seedling abundance for each site.

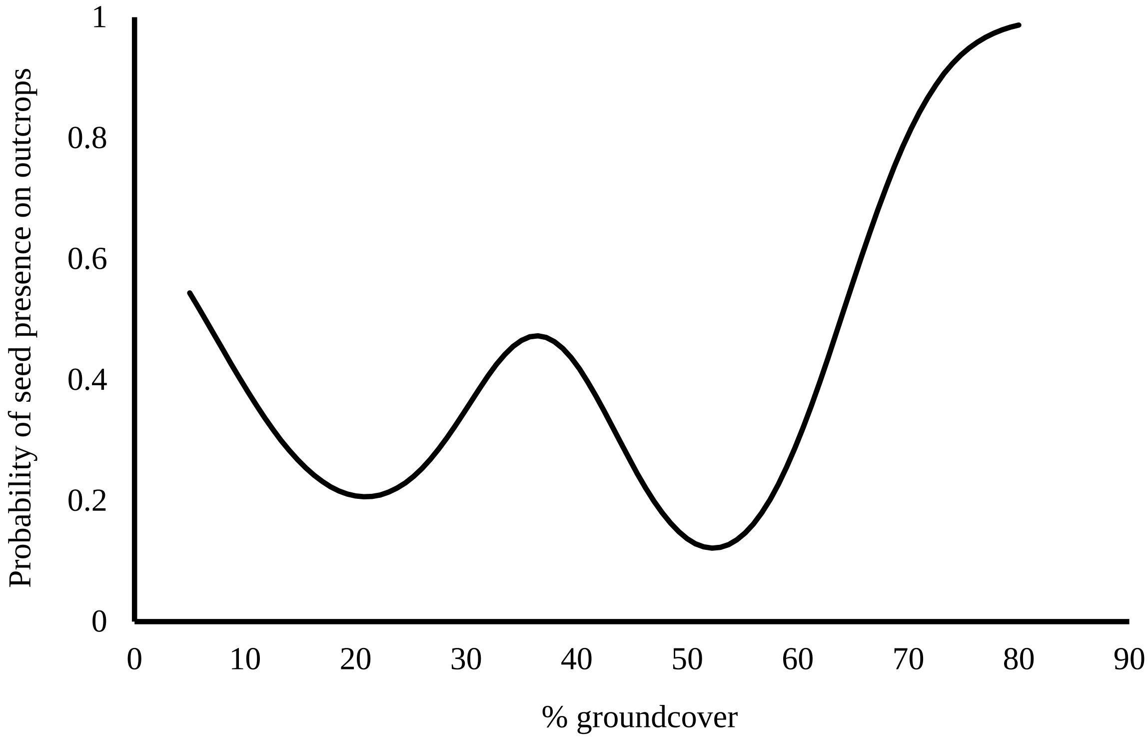


Fig. 6. Probability of *C. sempervirens* seed presence in relation to groundcover for at outcrop sampling locations using nonparametric multiplicative regression in HyperNiche 2.0 (n = 28). The smoothed curve was generated from scatterplots using a locally weighted mean.

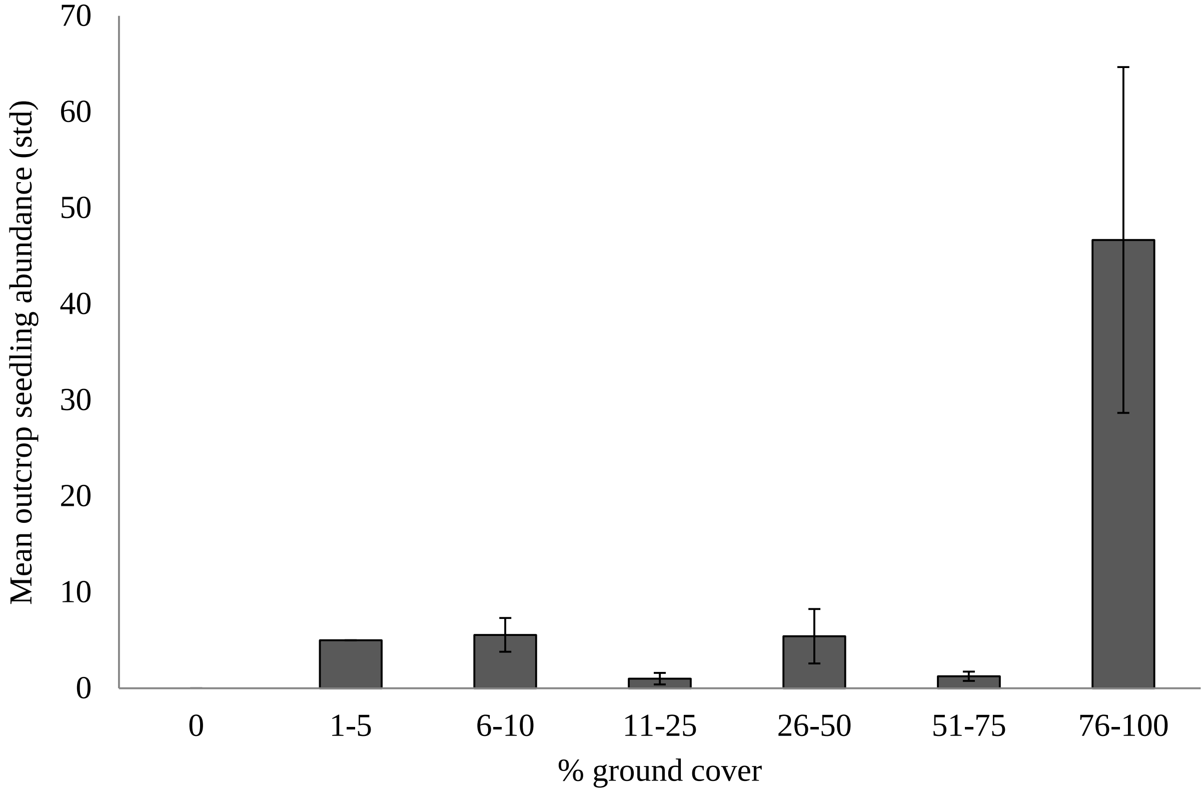


Fig. 7. Mean *C. sempervirens* (std) outcrop seedling abundance versus percent groundcover classes at rock outcrop sampling locations (n = 28). Seedling abundance was determined by seedling emergence from approximately 2.75 liters of soil collected at sampling locations.

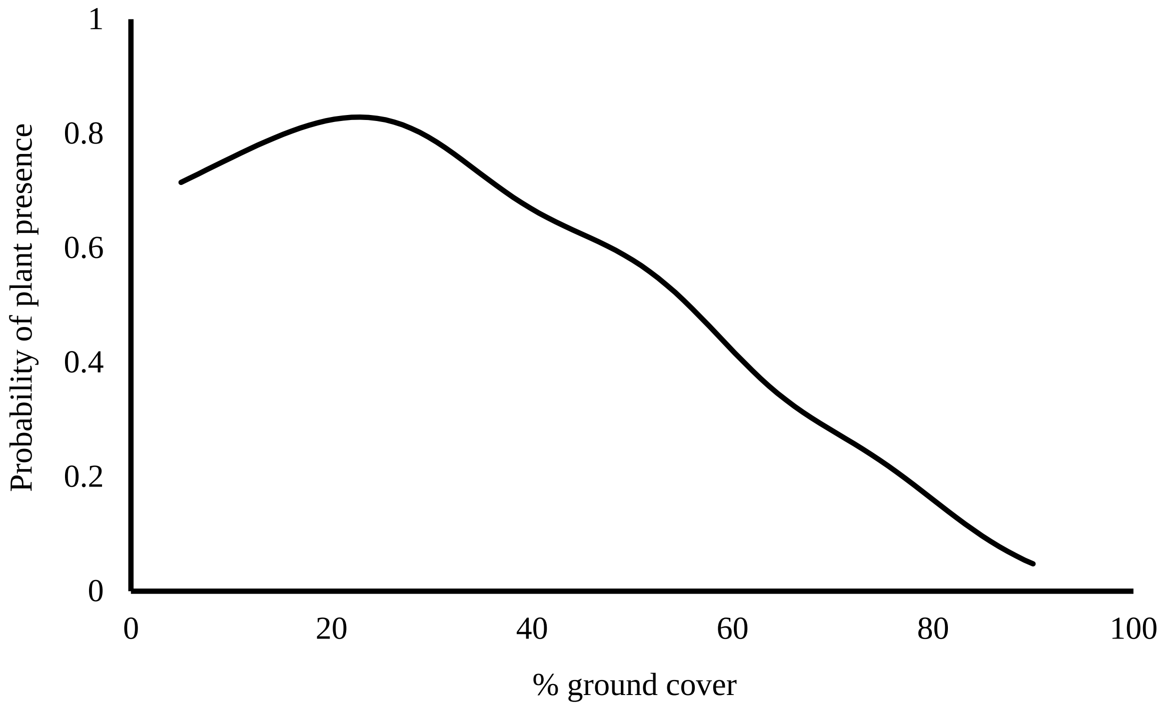


Fig. 8. Probability of the presence of above-ground *C. sempervirens* plants in relation to percent groundcover using nonparametric multiplicative regression in HyperNiche 2.0 (n = 144). The smoothed curve was generated from scatterplots using a locally weighted mean.

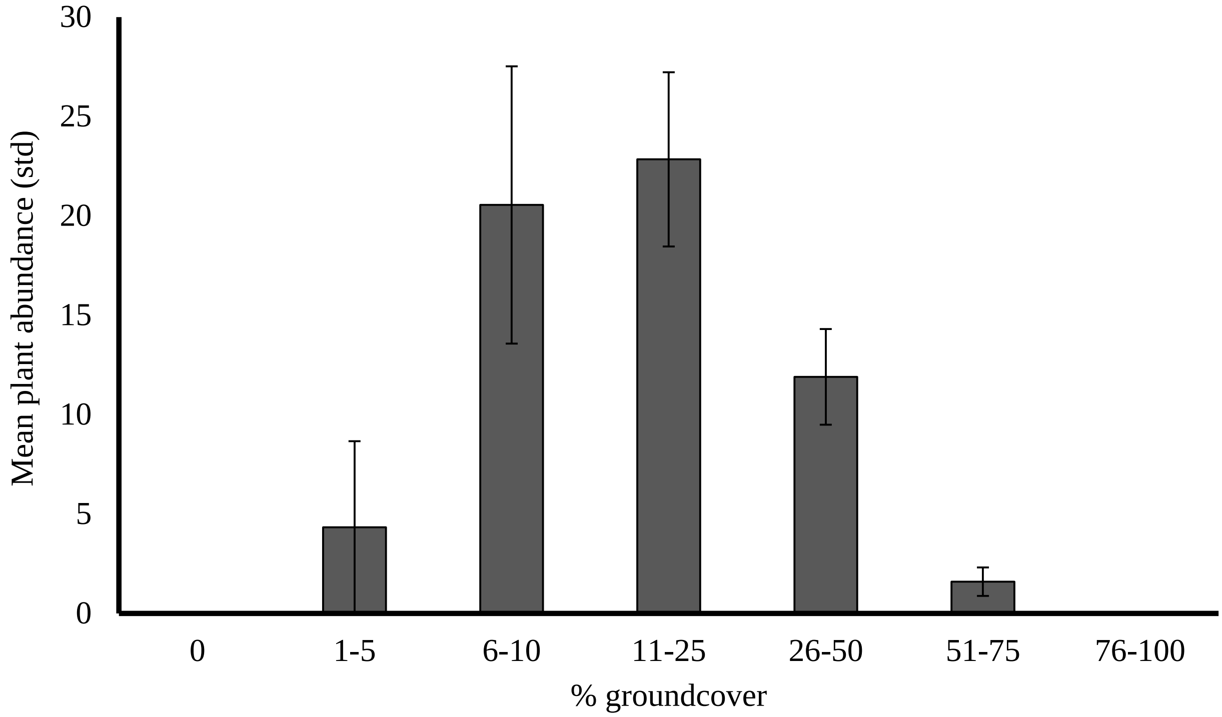


Fig. 9. Mean (SE) above-ground *C. sempervirens* abundance in response to groundcover classes within sample plots at rock outcrop sampling locations (n = 144).

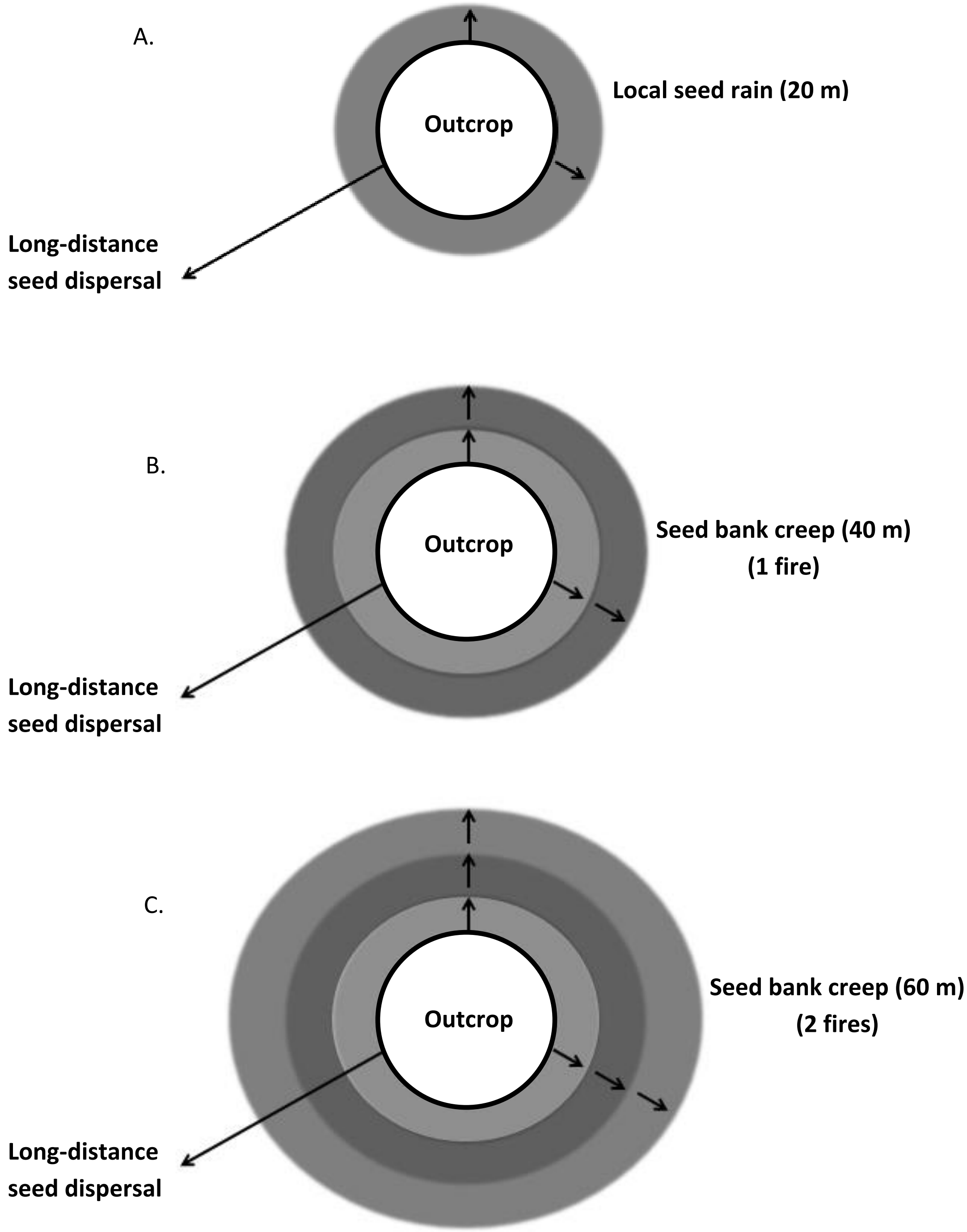


Fig. 10. Simplified seed bank creep model. A) Local seed rain increases seed presence ≤ 20-m from outcrop habitat while less-common secondary dispersal events lead to long-distance dispersal within the greater forest matrix. B) In the event of a stand-altering fire, the seeds produced from seedling germinated from local seed rain would allow the seed bank to creep in ≤ 20-m increments away from the outcrop and into the greater forest matrix. C) A second fire increases seed presence ≤ 60-m from the outcrop. In the event of successive fires, the creeping seed bank would link to seeds dispersed long-distance or neighboring outcrops.

APPENDIX A

Outcrop sample locations (UTM, NAD 1983, Zone 16), area (m^2), adult *C. sempervirens* abundance, and seed pod abundance (per 10 m radius plot).

ID	Easting	Northing	Area (m^2)	Adult abundance	Seed pod abundance	ID	Easting	Northing	Area (m^2)	Adult abundance	Seed pod abundance
1	464317	5161272	781	23	102	46	463943	5162367	335	4	91
2	464414	5160961	3750	0	0	47	463871	5162386	138	5	46
3	464514	5160940	2164	54	1020	48	463625	5162360	734	0	0
4	464641	5161033	438	22	211	49	463893	5162387	128	10	686
5	464596	5160792	604	0	0	50	463793	5162465	220	52	562
6	464538	5161010	1537	23	355	51	463659	5162442	103	0	0
7	464350	5161030	341	5	67	52	463578	5162412	179	40	473
8	465536	5160957	385	3	24	53	463654	5162520	83	0	0
9	465395	5160984	484	5	112	54	462836	5161675	492	37	210
10	465347	5160988	231	34	798	55	462713	5161290	5000	0	0
11	465267	5160983	181	19	353	56	462502	5161349	5587	0	0
12	465189	5161077	393	3	21	57	462365	5161341	4175	0	0
13	464983	5161176	704	4	7	58	462423	5161258	428	0	0
14	465120	5161085	842	2	18	59	461997	5161327	807	0	0
15	464993	5161109	610	1	0	60	461953	5161460	492	0	0
16	465011	5161185	232	11	62	61	461589	5161580	5	3	8
17	465053	5161081	2212	96	76	62	462644	5161659	1069	3	11
18	465183	5161112	302	4	155	63	463526	5161688	529	34	250
19	465147	5161218	570	0	0	64	463333	5161648	127	0	0
20	464997	5161371	4446	50	818	65	463347	5161742	1636	0	0
21	464798	5161379	720	4	41	66	463409	5161833	3905	0	0
22	464876	5161405	1560	0	0	67	463457	5161839	276	32	311
23	464727	5161548	245	12	120	68	463497	5161711	172	13	91
24	464772	5161395	215	0	0	69	463442	5161616	289	9	183
25	464721	5161486	5309	0	0	70	463651	5161848	6365	0	0
26	464511	5161333	294	1	40	71	464104	5161195	220	34	505
27	464738	5161388	349	0	0	72	463958	5161227	754	10	150
28	464917	5161384	152	24	608	73	464523	5161434	13461	37	424
29	464592	5161297	917	13	220	74	464544	5161570	191	13	266
30	464926	5161185	215	0	0	75	464525	5161541	172	13	350
31	464929	5161213	60	0	0	76	464464	5161694	11432	7	103
32	464328	5161336	268	41	343	77	464100	5162126	10617	30	618
33	464396	5161395	198	98	1430	78	464210	5162097	216	0	0
34	464512	5161261	3058	1	67	79	464283	5162125	214	14	280
35	464466	5161383	43	36	481	80	464371	5162082	105	0	0
36	464263	5161234	523	23	464	81	464012	5162991	1814	0	0
37	464211	5161211	230	10	178	82	463826	5163123	251	37	311
38	464389	5161346	70	7	101	83	464072	5162928	402	0	0
39	464593	5161405	342	0	0	84	464060	5162958	695	1	25
40	463752	5162344	2136	0	0	85	464072	5162996	178	12	104
41	463726	5162309	432	0	0	86	463998	5163099	318	107	564
42	463661	5162316	1052	38	920	87	463899	5163140	136	15	158
43	463705	5162269	158	24	202	88	463960	5163011	545	0	0
44	463800	5162368	161	20	312	89	464053	5163053	253	18	77
45	463901	5162350	246	0	0	90	464012	5163029	934	116	1469

APPENDIX A, CONTINUED

ID	Easting	Northing	Area (m^2)	Adult abundance	Seed pod abundance	ID	Easting	Northing	Area (m^2)	Adult abundance	Seed pod abundance
91	463882	5163121	143	15	190	136	461112	5163000	638	24	205
92	463446	5163793	1053	17	151	137	461111	5162873	380	10	196
93	463235	5163782	647	1	59	138	461220	5162947	4613	8	51
94	463314	5163799	904	64	929	139	461148	5163080	661	0	0
95	463599	5163686	1255	19	471	140	461001	5162756	868	0	0
96	463503	5163702	1580	8	92	141	461054	5162819	545	7	197
97	463452	5163657	696	1	44	142	460804	5162825	214	0	0
98	463401	5163719	223	0	0	143	464079	5160587	663	3	53
99	462633	5163588	473	0	0	144	461097	5162812	420	0	0
100	462570	5163530	327	19	164						
101	462690	5163566	6221	1	7						
102	463018	5163667	1355	0	0						
103	463084	5163658	302	34	537						
104	462849	5163842	472	11	273						
105	462656	5163727	121	3	46						
106	462721	5163882	2480	2	56						
107	462651	5163806	1041	0	0						
108	462634	5163845	3078	0	0						
109	463765	5160809	173	9	101						
110	463779	5160932	617	3	42						
111	463830	5160707	374	0	0						
112	463830	5160596	1235	0	0						
113	463892	5160768	103	1	11						
114	464573	5160699	704	0	0						
115	464535	5160733	147	3	66						
116	464359	5160767	438	1	10						
117	464097	5160404	290	6	17						
118	464108	5160261	128	0	0						
119	465414	5160960	30	79	1759						
120	465448	5160968	127	37	315						
121	465483	5160960	49	103	1713						
122	465612	5160996	494	24	535						
123	465258	5161296	245	8	222						
124	465106	5161349	10199	0	0						
125	463673	5160986	278	0	0						
126	463759	5160897	505	0	0						
127	463728	5160915	356	0	0						
128	463758	5160962	360	9	51						
129	464423	5160712	739	0	0						
130	464315	5160791	188	25	483						
131	464262	5160787	493	0	0						
132	464271	5160840	61	5	78						
133	464227	5160987	1075	10	114						
134	464207	5160894	130	13	248						
135	461030	5163029	2411	0	0						

APPENDIX B

Outcrop seed bank sample locations (UTM, NAD 1983, Zone 16), *C. sempervirens* seed abundance (per 0.6 liters soil), adult *C. sempervirens* abundance, and seed pod abundance (per 10 m radius plot).

ID	Easting	Northing	Seed abundance	Adult abundance	Seed pod abundance
1	465098	5161076	0	96	76
2	464591	5161314	0	50	818
3	464240	5161231	0	0	0
4	463896	5162352	0	24	608
5	463942	5162364	0	13	220
6	463871	5162397	2	23	464
7	463584	5162355	0	0	0
8	463899	5162385	23	4	91
9	461990	5161334	0	5	46
10	461898	5161303	3	0	0
11	461550	5161546	0	10	686
12	463372	5161840	46	0	0
13	463472	5161842	0	0	0
14	464155	5162113	6	3	8
15	464218	5162101	0	0	0
16	464270	5162126	0	32	311
17	464363	5162080	2	34	505
18	463969	5163095	0	10	150
19	463824	5160707	1	7	103
20	461200	5162928	0	30	618
21	461143	5163084	0	0	0
22	464991	5161402	0	14	280
23	464872	5161400	10	0	0
24	464923	5161392	6	116	1469
25	465114	5161326	1	0	0
26	464114	5161188	0	0	0
27	463954	5161242	4	8	51
28	464400	5161720	0	0	0

APPENDIX C

Forest seed bank sample locations (UTM, NAD 1983, Zone 16) and seed abundance per 0.6 liters soil.

ID	Northing	Easting	Seed abundance	ID	Northing	Easting	Seed abundance	ID	Northing	Easting	Seed abundance
1	5162295	463905	0	47	5160572	463971	0	93	5163251	462611	0
2	5162293	463686	0	48	5160784	463992	0	94	5163020	462374	0
3	5162310	463853	0	49	5160619	463932	6	95	5163087	462104	0
4	5162352	463823	0	50	5160598	464061	1	96	5163263	462660	0
5	5162303	463759	0	51	5160580	463959	6	97	5163063	462705	0
6	5162326	463752	0	52	5160791	463982	0	98	5163474	463227	0
7	5162345	463834	0	53	5160648	464078	2	99	5161267	464310	0
8	5162335	463640	0	54	5160606	463985	1	100	5161257	465077	0
9	5162309	463788	0	55	5160543	463943	0	101	5161004	464481	0
10	5162283	463736	0	56	5160539	463895	0	102	5163631	462990	0
11	5161765	463669	0	57	5160761	464024	4	103	5163455	463236	0
12	5161932	463362	0	58	5160810	464479	3	104	5161283	465108	0
13	5161719	463683	0	59	5160925	464677	0	105	5163512	463256	0
14	5161756	463370	2	60	5160872	464539	0	106	5163634	462803	0
15	5161885	463929	0	61	5160838	464686	0	107	5163802	462536	0
16	5161706	463692	0	62	5160829	464462	0	108	5163869	462847	0
17	5161809	463864	0	63	5160846	464527	0	109	5161383	464372	0
18	5161840	463787	0	64	5160955	464562	0	110	5163794	462777	0
19	5161845	463826	0	65	5160912	464631	1	111	5163592	463267	1
20	5161830	463257	0	66	5160856	464544	5	112	5161345	464433	0
21	5161647	463406	0	67	5161027	464661	0	113	5163644	462890	0
22	5161682	463343	0	68	5160827	464671	0	114	5161370	464300	0
23	5161696	463395	1	69	5160797	464496	1	115	5163526	462525	0
24	5161831	463905	0	70	5160973	464686	0	116	5161255	465055	9
25	5161689	463471	0	71	5163178	462144	0	117	5161245	464427	0
26	5161887	463694	1	72	5163215	462146	0	118	5161065	464215	0
27	5161724	463775	0	73	5163159	462439	0	119	5161282	464039	0
28	5161704	463521	1	74	5162919	462391	0	120	5163925	462839	0
29	5161889	463348	0	75	5163168	462529	0	121	5161420	464342	0
30	5161779	463763	0	76	5163099	462304	0	122	5163676	462774	0
31	5161849	463766	0	77	5162841	462749	0	123	5160973	465064	0
32	5161695	463568	0	78	5163074	462532	0	124	5163475	462563	0
33	5161837	463768	0	79	5162800	461952	0	125	5163393	463030	0
34	5161817	463850	0	80	5162868	462025	0	126	5163998	462724	0
35	5160570	463928	0	81	5162945	462328	0	127	5160847	464963	0
36	5160857	464027	26	82	5162991	462231	0	128	5164296	463115	0
37	5160666	464013	1	83	5162976	462696	0	129	5163531	461636	0
38	5160444	464025	28	84	5163194	462523	0	130	5160581	464060	21
39	5160582	463862	6	85	5163064	462501	0	131	5163375	463894	0
40	5160656	464055	0	86	5163361	462469	0	132	5160932	463750	0
41	5160749	464042	3	87	5162980	462551	0	133	5161447	461970	2
42	5160498	463997	2	88	5163191	462375	0	134	5161170	464907	0
43	5160498	463960	4	89	5161960	462115	0	135	5160710	463688	16
44	5160815	464008	30	90	5163028	462116	0	136	5163100	463769	1
45	5160437	464015	0	91	5162531	461123	0	137	5161123	462077	0
46	5160713	464047	0	92	5162773	462718	0	138	5162893	464063	0

ID	Northing	Easting	Seed abundance	ID	Northing	Easting	Seed abundance	ID	Northing	Easting	Seed abundance
139	5161222	464943	0	185	5163784	462773	0	231	5163887	463013	0
140	5163293	463834	2	186	5163856	462912	0	232	5163091	463669	0
141	5160939	463784	0	187	5161277	462043	0	233	5162533	463954	0
142	5161324	462000	1	188	5161230	464024	2	234	5161754	464662	0
143	5160392	464088	1	189	5160498	464090	0	235	5161956	464452	0
144	5162994	463950	0	190	5163759	462851	0	236	5162331	464176	0
145	5161195	465143	0	191	5161091	461998	0	237	5163322	462361	0
146	5163061	463794	0	192	5161554	461665	10	238	5162119	462081	0
147	5161276	464595	0	193	5163675	462751	0	239	5162830	463293	0
148	5162985	463975	0	194	5161262	464920	0	240	5161667	464877	0
149	5163302	462664	0	195	5160373	464033	0	241	5162346	464262	0
150	5160904	463706	3	196	5163220	463762	0	242	5162661	463764	0
151	5160740	463730	0	197	5163162	463738	0	243	5161028	461913	2
152	5161361	464534	2	198	5161507	461620	2	244	5162817	463726	0
153	5162331	463665	0	199	5161020	463618	12	245	5163059	462707	0
154	5162338	463930	0	200	5161122	463617	0	246	5162702	464175	0
155	5160964	463706	0	201	5161364	461890	0	247	5163010	462743	0
156	5160985	463769	0	202	5163584	463495	0	248	5163033	462689	0
157	5161268	462089	2	203	5163642	463301	0	249	5163004	461733	0
158	5161112	464975	0	204	5163819	462911	0	250	5162458	464223	0
159	5162394	463639	0	205	5163078	463693	0	251	5161582	465220	0
160	5161235	464187	0	206	5160525	464012	0	252	5161921	461564	0
161	5163370	463915	0	207	5161430	461581	0	253	5162510	464064	0
162	5161199	464327	14	208	5160579	463894	0	254	5162755	463809	0
163	5162381	463973	0	209	5162697	461351	0	255	5163242	462441	0
164	5163789	463397	0	210	5161099	463606	0	256	5163037	461583	0
165	5161415	461929	0	211	5162758	461380	0	257	5162517	464093	0
166	5160450	464100	1	212	5163842	463623	0	258	5162769	463506	0
167	5161114	463787	6	213	5162893	461488	0	259	5162786	463868	0
168	5162314	463961	0	214	5162885	463885	0	260	5161786	461328	0
169	5162402	463696	0	215	5161076	463720	3	261	5162717	461455	0
170	5161185	465140	1	216	5162771	461199	0	262	5163026	462789	0
171	5162956	461256	16	217	5162787	464104	0	263	5163389	462050	0
172	5160807	463736	0	218	5162317	464248	0	264	5163172	461759	0
173	5162906	461156	0	219	5162693	461119	0	265	5162043	461794	0
174	5163126	463722	0	220	5163215	462599	0	266	5162759	461848	0
175	5162838	461134	0	221	5162786	461398	0	267	5163408	462032	0
176	5162808	461325	0	222	5163561	463674	0	268	5162317	462628	0
177	5163622	462756	0	223	5163976	462863	0	269	5161741	465246	0
178	5163593	463140	0	224	5162756	464175	0	270	5162488	462624	0
179	5162315	463766	0	225	5161063	463743	0	271	5160806	462886	0
180	5161302	464423	6	226	5161599	461671	11	272	5162876	462618	0
181	5161357	464443	0	227	5161656	464838	0	273	5163577	460837	0
182	5161293	464404	63	228	5162923	461508	0	274	5163602	461766	0
183	5163163	463843	0	229	5161552	465016	0	275	5160748	462322	0
184	5160998	463636	9	230	5161087	461893	1	276	5162811	463465	0

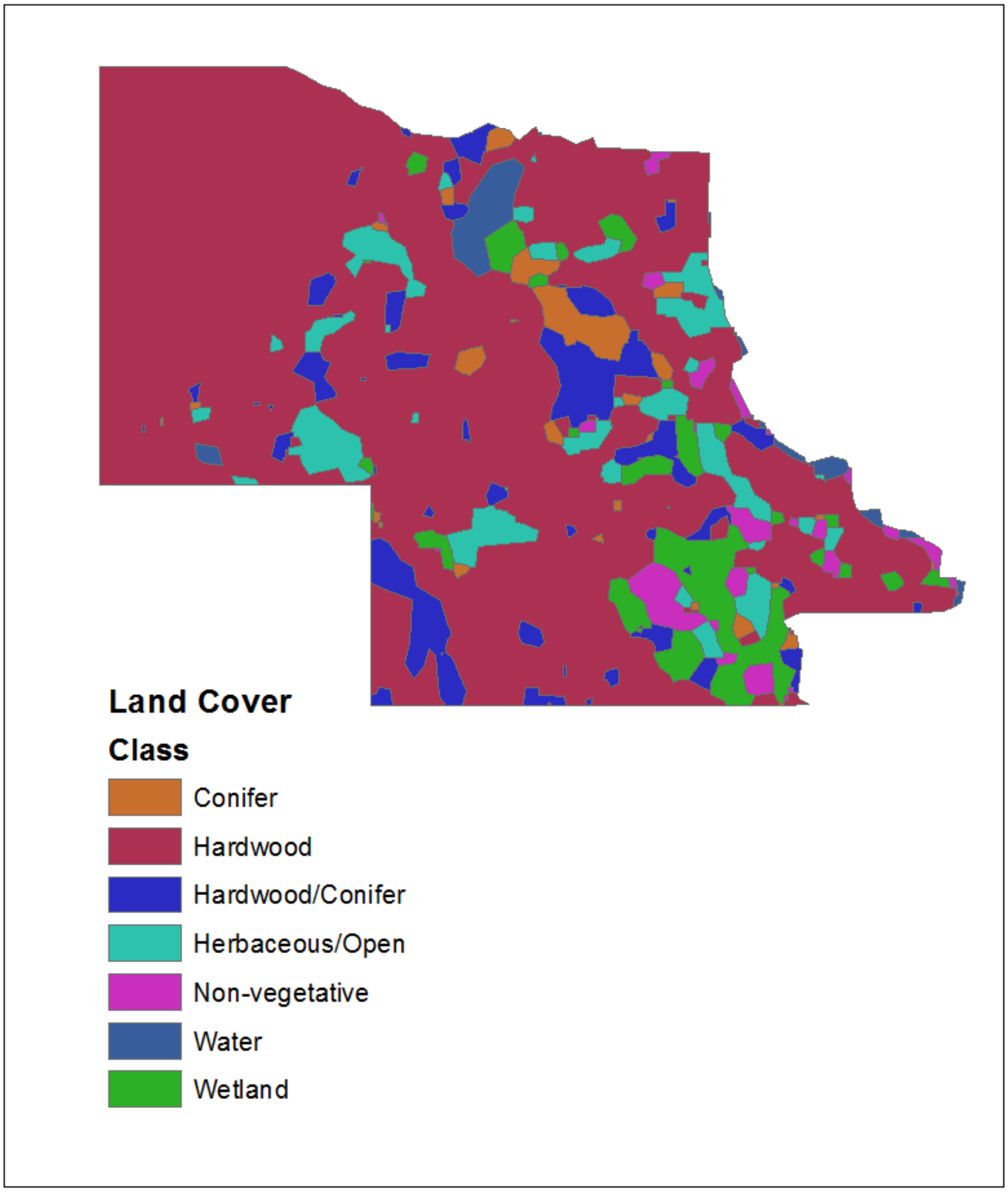
APPENDIX C, CONTINUED

ID	Northing	Easting	Seed abundance	ID	Northing	Easting	Seed abundance	ID	Northing	Easting	Seed abundance
277	5162149	461208	0	323	5162500	463782	4	369	5160530	463992	6
278	5162448	462202	0	324	5162445	463802	0	370	5160531	464014	0
279	5162050	461281	0	325	5162458	463833	0	371	5160537	464039	0
280	5163828	462044	0	326	5162463	463830	0	372	5160533	463987	6
281	5160801	462533	0	327	5162454	463811	0	373	5160524	464046	2
282	5161009	463090	0	328	5162449	463796	0	374	5160535	464002	4
283	5163516	461800	0	329	5162451	463806	0	375	5160949	464514	8
284	5162196	461557	0	330	5162473	463813	0	376	5160955	464439	2
285	5163632	461493	0	331	5161774	463449	0	377	5160956	464422	0
286	5162770	462940	0	332	5161800	463443	1	378	5160943	464514	28
287	5164205	462263	0	333	5161814	463412	3	379	5160964	464482	1
288	5163399	462023	0	334	5161779	463442	24	380	5160968	464466	3
289	5162411	462886	0	335	5161827	463416	1	381	5160954	464531	20
290	5162429	461670	0	336	5161820	463435	0	382	5160897	464560	16
291	5162399	462075	0	337	5161789	463402	4	383	5160915	464529	0
292	5164372	462728	0	338	5161796	463458	0	384	5160947	464524	3
293	5163662	461249	0	339	5161773	463397	0	385	5160975	464460	5
294	5161692	465274	0	340	5161793	463420	1	386	5160954	464475	0
295	5162631	461698	0	341	5161768	463403	0	387	5160956	464500	0
296	5164285	461026	0	342	5161772	463434	0	388	5160950	464432	2
297	5164154	460902	0	343	5161778	463423	0	389	5160909	464551	2
298	5162276	461625	0	344	5161775	463411	0	390	5160963	464462	1
299	5164175	461740	0	345	5161789	463433	0	391	5160926	464530	7
300	5164153	461436	0	346	5161800	463478	0	392	5161705	464261	0
301	5164161	461150	0	347	5162156	464209	2	393	5161539	463984	0
302	5164214	461413	0	348	5162208	464221	0	394	5161706	464173	0
303	5164336	460262	0	349	5162139	464238	2	395	5161617	464128	0
304	5164340	460708	0	350	5162126	464241	1	396	5161628	464121	0
305	5163758	461124	0	351	5162159	464185	11	397	5161639	464210	0
306	5164112	464160	0	352	5162181	464182	0	398	5161644	464111	0
307	5164218	460566	0	353	5162142	464229	1	399	5161569	464034	0
308	5164155	461602	0	354	5162181	464155	17	400	5161467	464032	0
309	5162610	462531	0	355	5162140	464272	0	401	5161719	464094	0
310	5164210	464186	0	356	5162199	464222	8	402	5161602	464304	0
311	5162760	462307	0	357	5160523	464057	0	403	5161448	463959	0
312	5163755	460811	0	358	5160517	464057	0	404	5161486	464043	0
313	5164266	461711	0	359	5160546	464033	2	405	5161719	464169	0
314	5163988	461182	0	360	5160524	463989	0	406	5161565	464309	0
315	5162477	463807	0	361	5160523	464005	0	407	5161594	464103	0
316	5162485	463774	0	362	5160513	464071	0	408	5161700	463983	0
317	5162465	463800	0	363	5160530	464053	0	409	5161676	464229	0
318	5162468	463784	0	364	5160535	464024	0	410	5161629	464087	0
319	5162498	463789	19	365	5160544	464009	0	411	5161544	463955	0
320	5162452	463823	4	366	5160526	464034	0	412	5161494	464055	0
321	5162467	463819	3	367	5160540	464016	0	413	5161666	464268	0
322	5162460	463826	0	368	5160518	464038	0	414	5161556	464060	0

ID	Northing	Easting	Seed abundance	ID	Northing	Easting	Seed abundance
415	5161667	464043	0	461	5161125	465086	0
416	5161573	463968	0	462	5161158	465131	0
417	5161654	463913	0	463	5161159	465173	0
418	5161508	463991	0	464	5161144	465093	0
419	5161731	464301	0	465	5161098	465114	18
420	5161472	464051	0	466	5161155	465102	0
421	5161751	464291	0	467	5161150	465183	0
422	5161634	463932	0	468	5161102	465160	0
423	5161656	463981	0	469	5161130	465193	0
424	5161468	464065	0	470	5161108	465150	1
425	5161556	463976	0	471	5161147	465158	0
426	5161546	464005	0	472	5161167	465180	0
427	5161698	464006	0	473	5161095	465150	0
428	5161564	464108	0	474	5161126	465161	1
429	5161760	464312	0	475	5161099	465097	5
430	5161716	464046	0	476	5162152	464194	0
431	5161675	464013	0	477	5160966	464377	3
432	5161649	464000	0	478	5160931	464457	2
433	5161653	464182	0	479	5160955	464414	7
434	5161635	463976	0	480	5162127	462557	0
435	5161775	463468	0	481	5161687	462856	9
436	5161844	463352	0	482	5161706	462821	0
437	5161774	463518	0	483	5161632	462674	0
438	5161760	463490	1	484	5161642	462679	0
439	5161754	463407	0	485	5161707	462667	0
440	5161754	463514	0	486	5161677	462883	0
441	5160964	464449	0	487	5161596	462676	0
442	5160949	464475	11	488	5161680	462926	0
443	5162205	464167	1	489	5161780	463045	0
444	5162185	464163	2				
445	5162164	464181	5				
446	5162184	464242	0				
447	5162167	464228	7				
448	5162215	464103	0				
449	5161744	464289	0				
450	5161633	464334	0				
451	5161700	464328	0				
452	5162177	464217	5				
453	5162201	464146	0				
454	5162180	464211	0				
455	5162189	464238	0				
456	5162159	464222	0				
457	5161133	465132	0				
458	5161164	465121	0				
459	5161141	465112	0				
460	5161135	465073	0				

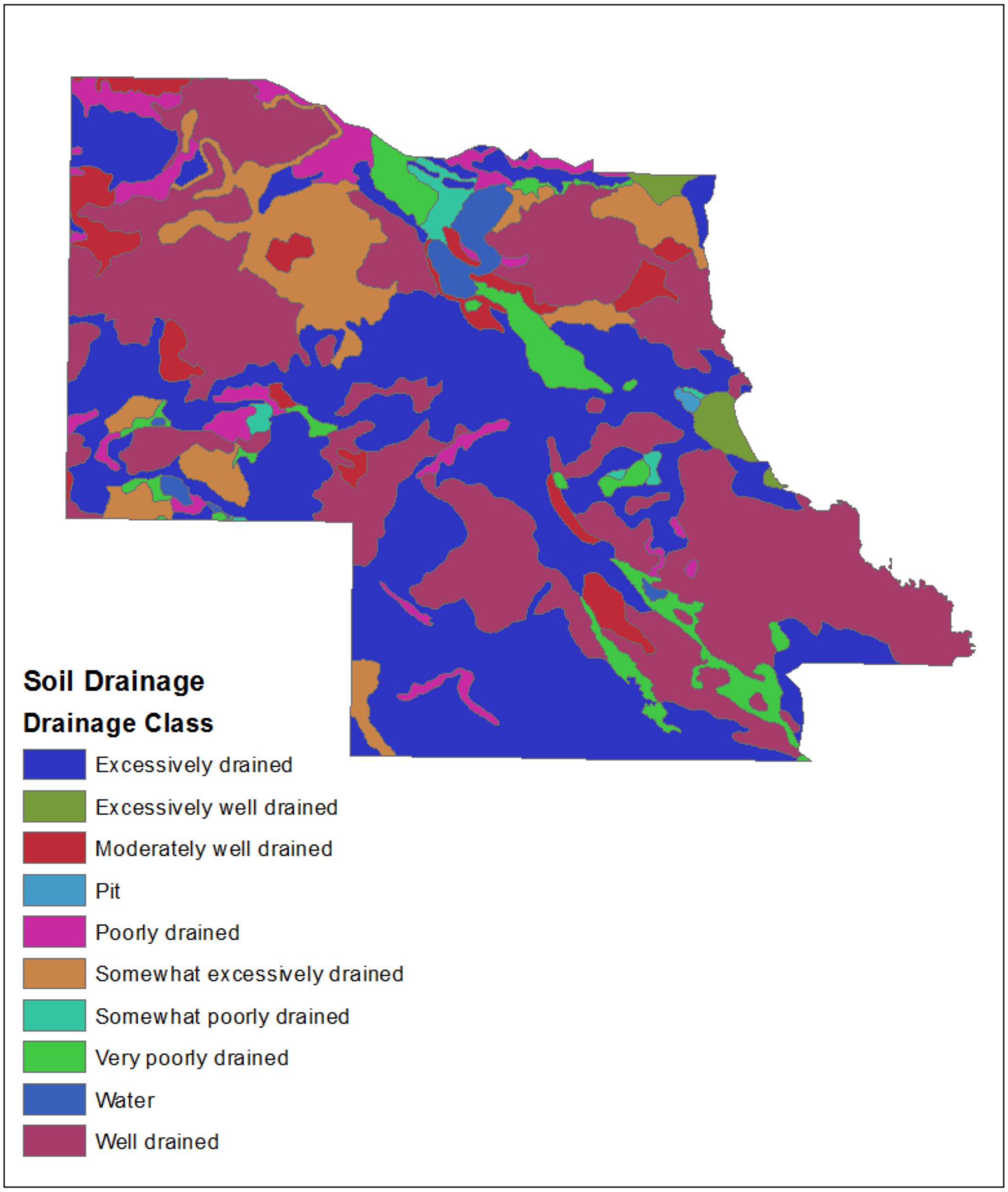
APPENDIX D

Land cover classifications extracted from a 2001 Marquette County land cover and use data set available from the Michigan Geographic Data Library (http://www.mcgi.state.mi.us/mgdl/). The original data set containing 30 classes was reclassified to include five classes: conifer, hardwood, hardwood/conifer, herbaceous, and non-vegetative.



APPENDIX E

Soil order extracted from a Marquette County SSURGO soils available from the Michigan Geographic Data Library (http://www.mcgi.state.mi.us/mgdl/).



APPENDIX F

Soil drainage class extracted from a Marquette County SSURGO soils available from the Michigan Geographic Data Library (http://www.mcgi.state.mi.us/mgdl/).