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RESEARCH ARTICLE

Dispersal limitation and seed predation drive rarity of a plant species at its range edge

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Abstract

1. Understanding the causes of species rarity is a central goal in ecology. The three filters thought to predict if a species is present or not in a community are the suitability of abiotic conditions, dispersal limitation and biotic interactions. Theory emphasizes the importance of the availability of abiotically suitable habitat in determining occurrence frequency, especially for species at their range edge, where the amount of suitable habitat is predicted to decline. However, the relative influence of these filters in driving species rarity is mostly unknown.
2. We used species distribution models (SDMs) to estimate habitat suitability based on broad-scale abiotic predictors for a rare plant species (*Stylophorum diphyllum*) at the northern edge of its global distribution. We tested the role of dispersal limitation by planting seeds in unoccupied sites that varied in their predicted habitat suitability and measured seedling emergence and seedling survival over 2 years. To manipulate the biotic interactions, we excluded seed predators by caging half of the seeds. We also measured the microclimate at each microsite, including soil moisture, temperature and canopy cover.
3. The habitat suitability estimated by the SDMs did not predict seedling emergence or short-term seedling survival. We found that dispersal limitation coupled with seed predation was a significant predictor of seedling emergence, while microclimate, specifically microsite temperature, was a significant predictor of short-term seedling survival.
4. *Synthesis*. Contrary to the assumption that species occur at a low frequency near their range edges due to a lack of suitable habitat, we found that dispersal limitation coupled with biotic interactions can drive rarity. If this is the case for many rare species at risk of extinction at their range edges, effective conservation strategies must incorporate assisted dispersal (i.e. translocations) into appropriate microsites and the management of biotic interactions to establish new populations and ensure long-term persistence.

KEYWORDS

community assembly, community theory, conservation, habitat suitability, rare plant, SDM, seed addition, species at risk, species distribution model, translocation

1 | INTRODUCTION

Understanding why many species are rare has long been a central goal in ecology. The frequency of occurrences within a species' range is one of the axes upon which rarity can be measured, in addition to local abundance (Gaston, 1994; Rabinowitz, 1981). For example, some rare species have large population sizes where they occur, but relatively few occurrences within their geographic range. In comparison, other rare species occur more frequently within their range but have small populations. In the case of the former, two primary processes are thought to limit the frequency of occurrences: low availability of sites with suitable conditions (abiotic and biotic) and the ability of the species to access those sites (dispersal; Moore & Elmendorf, 2006).

First, abiotic factors may cause a species to be infrequent on the landscape if its required conditions are restricted, reflecting its fundamental niche (Grinnell, 1917). Species that have evolved to specialize in a narrow range of abiotic conditions will occur infrequently. For example, plant species adapted to geological formations restricted to a few areas will occur only in those areas (e.g. Allison & Stevens, 2001). In addition, even habitat generalists that occur frequently near the centre of their geographic range may become less frequent near their range edges if the combination of environmental conditions they require becomes limited to small isolated pockets or if overall habitat quality gradually decreases towards the periphery (Brown, 1984; Holt et al., 2005; Holt & Keitt, 2000). However, few studies quantitatively assess the abiotic conditions at central and peripheral site locations in the field (Pironon et al., 2017).

Second, poor dispersal ability can prevent a species from arriving at a site, even if the habitat is suitable. The ability of a species to disperse and colonize can determine its frequency of occurrence. In addition, if a species can disperse quite far, but rarely does so, this can prevent it from recolonizing sites where a population was extirpated (Baur, 2014). Low dispersal rates may result from seed limitation, which can include a lack of seed availability (Clark et al., 2007; Seabloom et al., 2003). Additionally, dispersal barriers, such as those created by habitat fragmentation, can reduce colonization rates and exacerbate the effects of dispersal limitation (Primack & Miao, 1992). Dispersal limitation can be tested by adding propagules or mature individuals of a species to unoccupied sites. Many seed addition trials have provided evidence for dispersal limitation by documenting successful recruitment in formerly unoccupied sites (e.g. Clark et al., 2007; Ehrlén & Eriksson, 2000; Primack & Miao, 1992; Turnbull et al., 2000).

Lastly, even if a species can disperse to a site with favourable abiotic conditions, biotic interactions can prevent site occupation. Species may be limited in accessing suitable habitat if natural enemies (i.e. competitors, predators, parasites and pathogens) are present. The lack of a specific mutualist partner or pollinator can also prevent species from occupying otherwise suitable sites (Kraft & Ackerly, 2014; Williamson, 1996). For example, some orchid species require specific mycorrhizal fungi to germinate and survive (Hemrova et al., 2019; Reiter et al., 2016). Overall, biotic factors have been understudied relative to abiotic factors as the causes of species occurrence patterns (Ge et al., 2024; Lamothe et al., 2019; Wisz et al., 2013).

Understanding the relative influence of dispersal limitation, abiotic conditions and biotic interactions on limiting species occurrences is especially important for species of conservation concern close to their range-edge because it is often unknown why they are rare. They may have few occurrences due to being near their range edge, where suitable habitat may be less abundant (patchy) and/or of lower quality (Brown et al., 1996), or their rarity may be related to a lack of time and/or a limited ability to disperse within and beyond their range edge (Svenning & Skov, 2004). Anthropogenic habitat fragmentation exacerbates both factors by eliminating suitable habitat and increasing distances between the remaining suitable sites. Uncertainty about whether or not range-edge populations were always rare, even before extensive anthropogenic disturbance, has led to controversies about the need to conserve peripheral populations (e.g. Fraser, 2000; Hunter & Hutchinson, 1994) For example, Lesica and Allendorf (1995) suggest peripheral populations should only be conservation priorities if they exhibit genetic divergence from central populations.

In our study, we test the influence of dispersal limitation, abiotic conditions and biotic interactions on the occurrence of the wood-poppy (*Stylophorum diphyllum* (Michx.) Nutt.; Paperveraceae), an endangered herbaceous perennial with only five known occurrences at the northern edge of its range in southern Ontario, Canada (Government of Canada, 2021). Species distribution models (SDMs) suggest there is an abundance of potentially suitable, unoccupied habitat existing in the region (McCune, 2019). The species relies primarily on ants for dispersal, which may limit its ability to colonize sites with suitable habitat, in addition to facing seed predation from rodents (Bowles, 2007).

We used a seed addition trial to experimentally test the relative influence of dispersal limitation, abiotic conditions and biotic interactions on *S. diphyllum* occurrence. First, we estimated the suitability of broad-scale abiotic habitat using an SDM and planted seeds in unoccupied forested sites with variable habitat suitability ratings. We measured canopy cover, soil moisture and temperature at the planting microsites. To manipulate the biotic interactions, we excluded seed predators by caging half of the seeds. If dispersal limitation is the main limiting factor, we predicted relatively high rates of seedling emergence and survival regardless of predicted habitat suitability. If the availability of broad-scale suitable habitat is the main cause of the rarity of *S. diphyllum*, we predicted that seedling emergence and survival rates would be positively correlated with habitat suitability. If fine-scale microclimate conditions are more important than broad-scale habitat suitability, we predicted that microsite conditions would be a stronger predictor of seedling emergence and survival or that they might interact with broad-scale habitat suitability. For example, seedling emergence rates could be high in low suitability sites, but only if planted in a suitable microsite. Finally, if seed predators limit occurrences, we predicted higher rates of seedling emergence in exclosures compared to unprotected controls.

2 | METHODS

2.1 | Study species

Stylophorum diphyllum is a long-lived herbaceous perennial that occurs in moist deciduous forests and in forested ravines and slopes near streams (COSEWIC, 2007). Flowering occurs late April through May and capsule fruits are produced in late May to mid-June through self-fertilization or cross-pollination (Figure S7; COSEWIC, 2007). Each capsule contains an average of 68 seeds per capsule (between 1 and 146 seeds; personal observation), and each seed is about 2.5 mm long and 1.5 mm wide with an elaiosome (Gunn, 1980; Gunn & Seldin, 1976). Seeds are ant-dispersed (Bowles, 2007) and are also sometimes moved by small slugs (personal observation). *Stylophorum diphyllum* is critically imperilled (S1) near its leading range edge in Ontario and its rear range edge in the states of Georgia and Alabama in the United States (NatureServe, 2023). In Ontario, it was first collected in the late 1800s and not re-discovered for nearly 100 years (1987; Bowles, 2000). Only four populations were known as of 2010, all within 30 km of the city of London, and a fifth population was discovered in 2015 (McCune, 2019). Threats to the wild populations in Canada include small population sizes with low recruitment, erosion and fill, adjacent land use change and recreation pressure (Bowles, 2007). In addition, mice eat the seeds (Bowles, 2007). However, despite its rarity in Canada, *S. diphyllum* is locally common and found in abundance with many occurrences in West Virginia, Kentucky and Ohio.

2.2 | Study area

Our study area is located within the Mixedwood Plains ecozone (Figure 1). This is Canada's most densely populated ecozone, exemplified by high land conversion and habitat fragmentation (Crins et al., 2009). It has phanerozoic calcareous bedrock and a mild climate, with average daily temperatures around 17°C in summer and −5°C in the winter, and moist conditions (720–1000 mm rainfall/year; Crins et al., 2009). The southernmost part of the Mixedwood Plains contains the Carolinian zone, a biodiversity hotspot dominated by hardwoods (i.e. oaks, hickories and maples) and a rich diversity of plant and animal species found nowhere else in Canada (Oldham, 1990). Most forests in this region are privately owned, although small provincial parks and nature reserves can be found throughout (Government of Ontario, 2021).

2.3 | Experimental design

To estimate broad-scale habitat suitability across southern Ontario, we used an SDM based on 14 environmental predictors created by McCune (2019). The SDM used MaxEnt (version 3.3.3 k), which performs well even with very few occurrences (Hernandez et al., 2006; Phillips et al., 2006). MaxEnt predicts the habitat suitability of each cell across the study extent based on the locations of known occurrences and their associated environmental conditions. The occurrence records were sourced from the Ontario Natural Heritage Information Centre (NHIC) and one new record (2015) from McCune's plant survey ($n = 5$). The SDM used a resolution of one-hectare (100 m × 100 m grain size; Figure S1) and MaxEnt default settings, except the regularization parameter was set to 0.5. We used MaxEnt's cumulative output, with 0 indicating very low suitability and 100 indicating the highest suitability. Range-edge occurrences are often better predicted by SDMs built at the extent of the range-edge only (Luoto et al., 2005; Stockwell & Peterson, 2002). However, due to the low number of occurrences in Ontario, we compared the results to a range-wide SDM (Wiedenfeld, 2025) built at the same resolution but with an extent encompassing all *S. diphyllum* occurrences ($n = 1329$) in North America (GBIF.org, 2023; see Methods S1; Table S1; Figure S2).

Due to the very small number of *S. diphyllum* occurrences in the study region, we did not have independent presence records with which to test the utility of the SDMs. However, we have confidence that the range-edge only SDM provides a reasonable assessment of habitat suitability based on plant community surveys of 295 one-hectare grid cells across southern Ontario (Methods S2). Grid cells with predicted suitability greater than the lowest suitability of an occupied site (37.8%) had significantly higher relative abundance and number of common associated species of *S. diphyllum* than sites below that threshold (Methods S2; Results S1; Table S2; Figures S3 and S4). In contrast, we found no significant difference in relative abundance and total number of common associates between sites predicted to be suitable versus unsuitable by the range-wide SDM (Results S1).

To test the effect of broad-scale habitat suitability on recruitment from seed, we selected nine, one-hectare unoccupied sites (each corresponding to an SDM grid cell) in two different properties owned by the Nature Conservancy of Canada (NCC). Three sites are located within a property located about 100 km southeast of the city of London, ON, comprised of mostly Carolinian forest (44 ha total), and six sites are located at a second property, located approximately 90 km northwest of London, comprised mostly of upland hardwood forest (71 ha). At each property, we selected sites for planting with the aim of representing a range of predicted suitability (Figure S1). The nine selected sites range from 14.23% to 70.42% predicted suitability. We chose sites based on the following criteria: (1) The majority of the site was ecologically similar habitat to wild populations (i.e. we excluded sites with >50% pine plantation), thickets or non-forest land (i.e. agricultural fields), (2) the site was accessible and relatively close to a trail and (3) the site had no apparent threats (i.e. evidence of high herbivory rates, encroaching developments). Within each site, we placed nine plots, selecting the locations non-randomly with the aim of maximizing the range of canopy light and soil moisture levels. We avoided placing plots directly in standing water (i.e. creeks) or directly on trails.

We collected seeds ($n = 109$) in late June 2019 from two in situ mother plants of one wild population (one fruit from each plant),

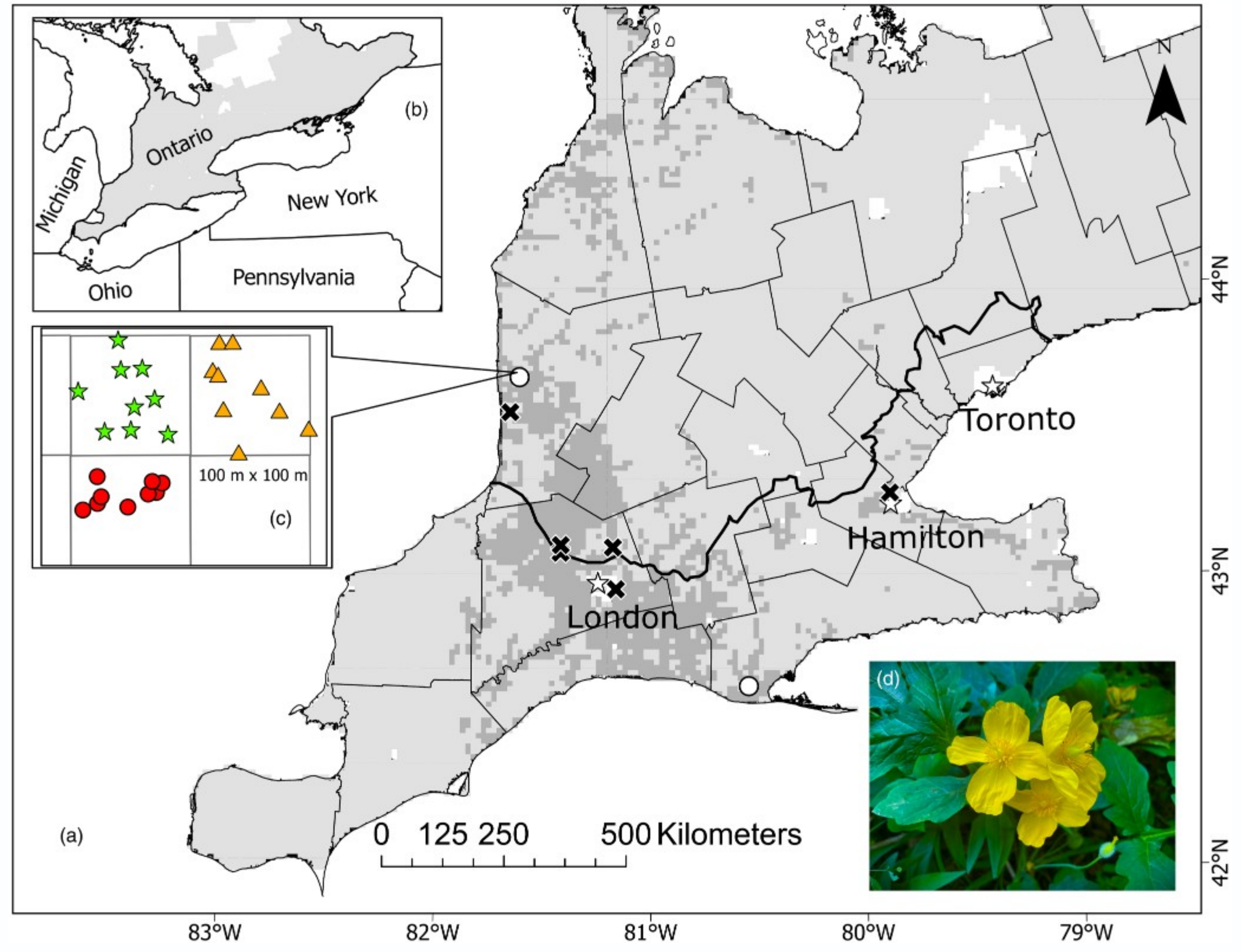

FIGURE 1 Study area in Ontario, Canada. Panel (a) the thin lines represent county borders, and the thick black line shows the approximate northern boundary of the Carolinian zone. Dark grey shading shows areas predicted by the range-edge species distribution model (SDM) to be suitable for *Stylophorum diphyllum* based on the minimum suitable threshold of 37.9%. Suitable areas have been generalized to 2 km × 2 km cells to increase visibility. Light grey shading shows the extent of the SDM. Circles indicate the location of seed addition properties. Crosses indicate the wild populations and one historically translocated population (near Hamilton). Major cities are represented by stars. Panel (b) the entire SDM extent in Ontario (grey shading) and its location in relation to neighbouring states. Panel (c) one planting property. Thin lines represent the 100 m × 100 m site boundaries and coloured shapes indicate seed addition plots. High SDM-estimated habitat suitability is represented by green stars, intermediate suitability by orange triangles, and lower suitability by red circles. Panel (d) *S. diphyllum* in bloom with a fruit forming in lower right corner (Picture by Author).

much less than 10% of the population's total seed production, as recommended by the CPC (Center for Plant Conservation, 2019). We registered seed collection with the Ontario Ministry of Natural Resources and Forestry as *Possession for Scientific or Educational Purposes by an Educational Organization* (s.23.15) under the Ontario Endangered Species Act. We then planted these seeds in growth chambers in 2020 as part of a germination trial and greenhouse common garden experiment (Reiter & McCune, 2023). To obtain seeds for the current seed addition experiment, we harvested fresh seed from 45 adult plants that resulted from the common garden trial starting in late February 2021 until mid-June 2021, and stored seed in moist sand at approximately 5°C until planting. This ensured an abundant number of seeds for our trial with minimal impact on the wild populations. We sorted the seeds to ensure each plot received the same relative abundance of seeds harvested in different weeks to account for any viability differences between seeds collected at different times during the 5-month harvest period. We also conducted a seed viability test in Petri dishes using a subset of 9–11 seeds from each collection week.

To simulate natural dispersal to the selected, unoccupied sites (breaking dispersal limitation), we planted all nine 1-ha sites over a 2-week period between late July and mid-August 2021, approximately 1 month after the natural seed release period. Before planting, we cleared plots of competing vegetation and removed leaf litter. At each of the nine selected plots within each site, we then carefully hand-planted 50 seeds with tweezers, dividing 25 seeds into each of two sub-plots (each sub-plot ~20 cm in diameter, ~30 cm apart), ensuring that the seeds were at least 2 cm apart and no more than ~3 mm deep. We expected recruitment to occur in spring 2022 because seeds are naturally released in the warm spring–summer months, overwinter and then germinate the following spring. To test the effect of seed predators (potential biotic limitation), we caged one sub-plot of each pair using a cage made with 23-gage steel mesh wire (¼ inch [0.635 cm] openings), which allows for invertebrate access but excludes mammals, including small rodents (Harrison et al., 2003). We formed each exclosure into a closed-cube shape (approximately 24 cm diameter and 30 cm high) and inserted each cage approximately 7.5 cm deep into the ground, secured with landscape staples (Figure S1).

To test for the effects of abiotic microsite differences, we measured soil moisture, canopy cover and temperature at each plot. To quantify soil moisture, we took the average of two soil moisture readings (one in each sub-plot, approx. ~1 m apart) with a Delta-T Devices SM150 two-prong soil moisture kit (model SM150T sensor with a HH150 metre set to the 'mineral soil' setting). To quantify light levels, we captured two canopy photographs with a clip-on smartphone fisheye lens attachment and using the freely available 'Gap Light Analysis Mobile App' (GLAMA) to estimate canopy cover, taking the average of two canopy cover index (CaCo) values (Gonsamo et al., 2013). The canopy cover index (%) estimates canopy cover by rescaling hemispherical photographs taken from a single position to perpendicular projections of light gaps in the tree canopy (Tichý, 2016). To quantify the microsite temperature, we deployed a Kestrel drop data logger in each plot (nine plots total per site), measuring the temperature every 0.5 h for at least two consecutive days between June and August at a height of ~40 cm (the average height of adult plants). We fitted each logger with an opaque, white plastic cup to serve as a solar shield and cut side slits for ventilation.

We did not have enough data loggers to measure all 81 plots at the same time. Therefore, we calculated the mean temperature at each plot ($n = 9$) within each one-hectare site for the same 69-h period. We then subtracted the mean of the site from the mean of the plot to obtain a 'temperature differential'. This effectively identifies planting plots that were hotter or cooler than the average of all plots in a site. To account for variability in weather conditions at different sites during the logger deployment, we standardized the raw plot differentials by dividing the raw plot differentials at each site by the site standard deviation. The raw differentials of the plot were highly correlated with these standardized differentials (Pearson's correlation coefficient; $r = 0.98$) and therefore we used the raw temperature differentials in all analyses.

We monitored the plots for early seedling emergence in late October 2021 and took two to three censuses throughout the 2022 growing season (late May to late July) to record the total number of emerged seedlings. We monitored again in late May to mid-June 2023 to record year-two survivorship. During each census, we removed any cages without seedlings and opened the tops of the cages with larger plants that could experience restricted growth.

2.4 | Statistical analyses

We modelled first-year emergence rates and year-two survival rates with generalized linear mixed models (GLMMs) with a binomial distribution (logit link). We modelled emergence with plots nested within site as random effects. We modelled year-two seedling survival with plot only as a random effect because site explained low variance in the response, resulting in singularity of the model fit. We used the predictors cage treatment, SDM-predicted habitat suitability, soil moisture, canopy cover index, and temperature differential (Table 1). We fitted soil moisture and canopy cover index with a quadratic term due to the expected hump-shaped relationship between these factors and emergence and survival rates. We took the natural log of soil moisture. In the year-one seedling emergence model, we used the highest number of emerged seedlings recorded out of 25 seeds planted in each

TABLE 1 Results of a generalized linear mixed effects model assessing potential predictors of first-year emergence rates of *Stylophorum diphyllum* seedlings.

Predictor	Coefficient	SE	df	AIC[a]	p[b]
(Intercept)	−3.65	2.44	n/a	644.19	n/a
Cage (yes)	4.65	0.78	1	n/a	n/a
SDM habitat suitability index	−0.01	0.01	1	643.24	0.306
Soil moisture (log)	0.93	1.60	1	n/a	n/a
Soil moisture (log)^2	−0.05	0.26	1	642.23	0.844
Canopy cover index	−0.02	0.08	1	642.25	0.809
Canopy cover index^2	0.00	0.00	1	642.19	0.978
Relative temperature differential	0.45	0.36	1	643.75	0.213
Relative temperature differential^2	−0.91	0.73	1	643.84	0.199
Cage × soil moisture (log)	−1.11	0.26	1	659.51	**<0.001**

[a] Akaike's information criterion (AIC) for the model that includes all factors except the one being tested. To respect marginality, we do not drop individual predictors that are also in an interaction (indicated as n/a for those predictors).

[b] p-values indicate the significance of each predictor using a likelihood ratio test. We did not drop individual predictors that were also in a significant interaction. Predictors with $p < 0.05$ are indicated in bold text.

sub-plot ($n=162$) as the response. We included 14 early recruits from fall 2021 that emerged in the same season as planting. We accounted for zero inflation by applying a single zero inflation parameter to all observations (each sub-plot), where the probability of producing a structural zero is equal for all observations. In the year-two survivorship model, we used the proportion of emerged seedlings (2022) that survived to year two (2023) at each sub-plot as the response, including only sub-plots that had at least one seedling emerge ($n=102$). We used Pearson's correlation coefficients to ensure that there were no strong pairwise correlations between predictor variables in either model.

We predicted that the broad-scale habitat suitability or the cage treatment could interact with microclimate factors to influence emergence or survival. Therefore, we included two-way interactions of cage treatment and SDM-predicted habitat suitability with each microclimate predictor in both models (Table 1). For example, if most uncaged seeds were predated, then the effects of broad-scale habitat suitability or abiotic microsite factors would be detectable only within cages. Similarly, if the SDM accurately predicts overall site suitability but emergence and/or survival require the right abiotic microsite within broadly suitable sites, then the SDM-predicted habitat suitability may interact with the conditions of the abiotic microsite. We also tested microclimatic predictors interacting amongst each other in the emergence model but dropped these interactions in the survivorship model because of model convergence issues due to fewer observations. We repeated the modelling procedure above using the predicted habitat suitability from the range-wide SDM instead of the range-edge only SDM (see Results S2; Tables S3 and S4; Figures S5 and S6).

We built all models with the 'glmmTMB' package (Brooks et al., 2017) in the software R (version 4.1.2; R Core Team, 2021). To test the significance of fixed effects and interactions while accounting for other predictors, we conducted single term deletion hypothesis testing using a likelihood ratio chi-square test to perform marginal fitting of terms (i.e., respecting the hierarchy of the terms) with the 'drop1' function in R. The test compares a model without the specified predictor to the full model using Akaike's information criterion (AIC). If the test on the full model showed some of the candidate interactions were not significant, we re-fitted the model without them so we could assess the importance of the individual predictors within the interaction. First, we dropped quadratic term interactions that were not significant, then re-fit the model and dropped non-quadratic interactions that were not significant. To measure the variance explained by each model, we extracted Nakagawa's pseudo-R^2 values (conditional and marginal) with the 'performance' package (Lüdecke et al., 2021). We checked for model specification errors using the 'DHARMa' package (Hartig, 2022). We confirmed that there is no spatial autocorrelation in the model residuals by plotting spline correlograms using the 'ncf' package (Bjornstad, 2020). We used the 'visreg' package to visualize the results of the model using partial regression plots, which show the effect of each predictor or interaction while holding all other predictors in the model constant (Breheny & Burchett, 2017).

In addition to GLMMs to test the relative importance of each predictor and interactions, we used SAS software to perform response surface regressions (SAS PROC RSREG) to estimate the combination of conditions that maximized and minimized emergence in 2022, and survival of emerged seedlings to 2023 (SAS Institute Inc, 2024). For the response first-year emergence, we modelled caged treatment separately because the response surface response curves cannot integrate categorical predictors. For year-two survival, we pooled caged and uncaged treatments because there was no significant difference in year-two survival inside versus outside of cages. We modelled the logit-transformed response where $\mu=$seedlings emerged in 2023 and $n=$seedlings emerged in 2022. The factors in the response surface model were the habitat suitability predicted by the range-edge SDM, soil moisture, canopy cover index, and temperature differential. We used ridge regressions (RIDGE MIN MAX) to explore the response surfaces. The ridge regressions identified the estimated ridges of the minimum and maximum responses based on the coded data, which indicate environmental optimums for emergence and year-two seedling survival.

3 | RESULTS

3.1 | Seedling emergence

Simulated dispersal via seed addition resulted in the emergence of seedlings at all one-hectare sites, representing a range of SDM-predicted habitat suitability. Seedling emergence at each sub-plot varied from 0% to 56% (mean $=2.95\pm0.27$ seedlings from 25 seeds). Only 479 seedlings emerged from 4050 total seeds planted (11.8%). The SDM-predicted habitat suitability index was not a significant predictor of seedling emergence rates, regardless of whether we used the range-edge only or range-wide SDM estimate (Figure 2; Figure S5; Table 1; Table S3). The only significant predictor of seedling emergence rates was the interaction between cage treatment and soil moisture (Figure 2; Figure S5; Table 1; Table S3). The cage treatment had a large effect on emergence rates. In total, 18.4% of seeds planted in caged sub-plots emerged compared to 5.1% in uncaged sub-plots. Predicted seedling emergence rates were much higher in caged sub-plots, except at the very highest levels of soil moisture (Figure 2). Overall emergence rates in the field were much lower than the rates we observed from our laboratory seed viability test (42.8%). However, field emergence rates neared this rate in caged sub-plots with lower soil moisture levels (Figure 2). The abiotic microsite variables, canopy cover index and the relative temperature differential, were not significant predictors of seedling emergence rates (Table 1). The model pseudo-R^2 values were 0.17 (marginal) and 0.27 (conditional).

3.2 | Year-two seedling survival

Overall seedling survivorship to year two was ~33% (159 survived to 2023 out of 479 seedlings that emerged in 2022) and 3.9% of all seeds planted in 2021 yielded a living seedling in 2023. As for

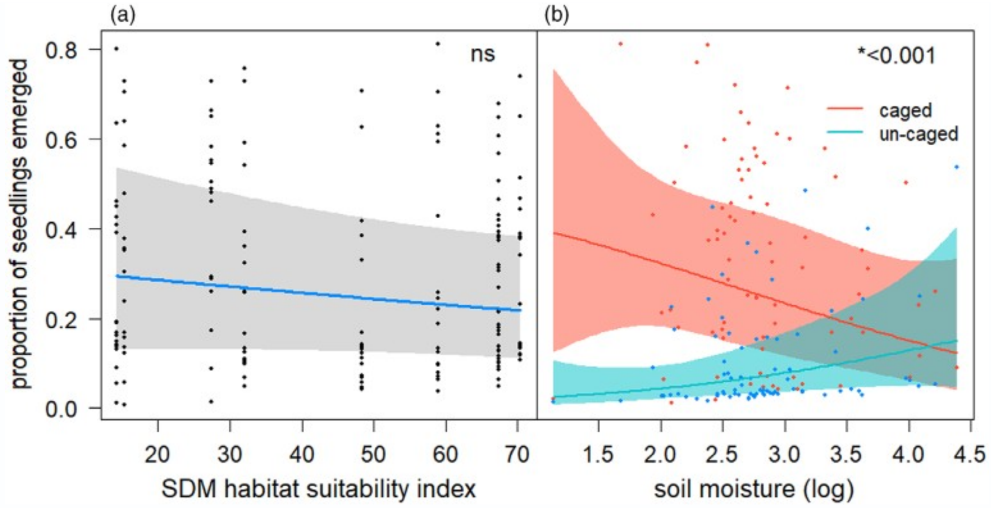

FIGURE 2 Partial regression plots showing the effect of (a) the species distribution model (SDM) habitat suitability index on seedling emergence (not significant) and (b) the interaction of cage treatment with soil moisture (log) on seedling emergence (significant; denoted by the asterisk). All other variables are held at the median (for continuous variables) and cage treatment is set to caged in panel (a). Thick coloured lines represent the prediction and shaded areas represent Wald 95% confidence intervals. Dots represent partial residuals.

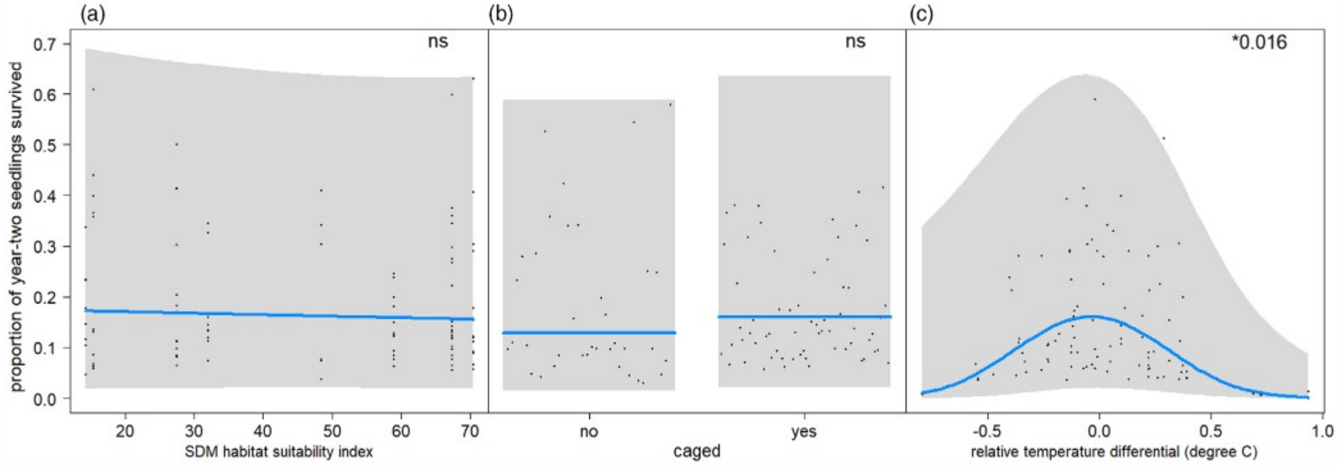

FIGURE 3 Partial regression plots showing the effect of (a) species distribution model (SDM) habitat suitability index (not significant), (b) cage treatment (not significant), and (c) relative temperature differential (significant; denoted by the asterisk) between plots on year-two seedling survival. In each panel, all other variables are held at the median (for continuous variables), and cage treatment is set to caged in panels (a, c). Thick blue lines represent the predictions and grey-shaded areas represent Wald 95% confidence intervals. Dots represent partial residuals.

seedling emergence, the SDM-predicted habitat suitability index was not a significant predictor of year-two seedling survival, regardless of whether we used the range-edge only or range-wide SDM estimate (Figure 3; Figure S6; Table 2; Table S4). The cage treatment also was not a significant predictor of year-two seedling survival, with 34.2% of seedlings surviving in caged sub-plots ($n = 128$) compared to 29.5% of seedlings ($n = 31$) surviving in uncaged sub-plots (Figure 3; Table 2). We found a significant hump-shaped relationship between year-two survival rates and relative temperature differential, where sub-plots with temperatures closer to the site average had higher survivorship than sub-plots with relatively hotter or cooler temperatures (Figure 3; Table 2). The other abiotic microsite factors, soil moisture and canopy cover index, were not significant predictors of year-two survival rates (Table 2). The model pseudo-R^2 was 0.15 (marginal) and 0.51 (conditional).

3.3 | Environmental optimums identified by response surface models

Response surface models showed that the optimal conditions for seedling emergence were quite different from the optimal conditions for survival to the second year (Results S2). For example, the maximum emergence rate occurred inside cages where the canopy cover index was 32% and soil moisture was 65%. In contrast, the maximum survival rate occurred where the canopy cover

TABLE 2 Results of the survivorship model assessing potential predictors for year-two survival of *Stylophorum diphyllum* seedlings.

Predictor	Coefficient	SE	df	AIC[a]	p[b]
(Intercept)	−7.50	7.60	n/a	303.91	n/a
Cage (yes)	0.25	0.33	1	302.49	0.448
SDM suitability index	−0.00	0.01	1	301.95	0.851
Soil moisture (log)	3.12	3.96	1	302.53	0.432
Soil moisture (log)^2	−0.54	0.67	1	302.58	0.412
Canopy cover index	0.20	0.23	1	302.78	0.348
Canopy cover index^2	−0.00	0.00	1	303.80	0.169
Relative temperature differential	−0.36	0.95	1	302.06	0.703
Relative temperature differential^2	−5.01	2.24	1	307.62	**0.016**

[a] Akaike's information criterion (AIC) for the model that includes all factors except the one being tested. To respect marginality, we do not drop individual predictors that are also in an interaction (indicated as n/a for those predictors).

[b] p-values indicate the significance of each predictor using a drop1 test. We did not drop individual predictors that were also in a significant interaction. Predictors with $p < 0.05$ are indicated in bold text.

index was 51% and soil moisture was 28%. The fitted response surface model explained 26.30% of the first-year emergence response under uncaged (cage = no) conditions ($R^{2\ \text{uncaged}} = 0.2630$) and 12.14% of the variance under caged (cage = yes) conditions ($R^{2\ \text{caged}} = 0.1214$). The fitted response surface model explained 22.19% of the variance of the survival to year two ($R^2 = 0.2219$). For more details, including uncaged maximum response conditions and caged minimum response conditions, see Results S2.

4 | DISCUSSION

We coupled a seed addition experiment with a SDM to disentangle the influence of dispersal limitation, abiotic habitat suitability and biotic interactions on the occurrence of a rare plant species near the edge of its geographic range. Community assembly theory places a large emphasis on abiotic habitat suitability filtering out species. In addition, it is hypothesized that near a species' range edge, a scarcity of sites with abiotic conditions within its fundamental niche results in low occurrence frequency (Brown, 1984; Holt & Keitt, 2000). Yet, we found that seedlings emerged and survived at all experimental sites, regardless of estimated relative habitat suitability. This suggests that a lack of available suitable habitat is not the main cause of rarity of *S. diphyllum* in southern Ontario, at least for these early life stages. Instead, dispersal limitation combined with seed predation are the main limiting factors for seedling emergence (Table 1; Figure 2), while microsite temperature influences seedling survival (Table 2; Figure 3). Dispersal limitation and seed predation could also influence the frequency of occurrences closer to the centre of *S. diphyllum*'s geographic range, where it is more common. Future studies could contrast the relative influence of these factors at different range positions. Nevertheless, our study shows that recovery strategies for *S. diphyllum* at its range edge must include assisted dispersal (i.e. translocations) coupled with seed protection in select microsites to ensure species persistence, rather than habitat protection alone. This may also be true for other plant species of conservation concern, especially near their range edge.

The fact that seedlings emerged at all experimental sites emphasizes the role of dispersal limitation in determining the frequency of occurrences, concordant with many other seed addition studies (Eriksson & Ehrlen, 1992; Seabloom et al., 2003; Turnbull et al., 2000). Our overall observed emergence rate (11.8%) is comparable to other seed additions of herbaceous understorey plant species (10.3%–33.8%; Ehrlén & Eriksson, 2000) and a global meta-analysis of seed addition trials (~15%; Clark et al., 2007). Only 3.9% of the seeds planted emerged and survived until year two, a rate comparable to short-term survival rates for other woodland perennials planted from seed. For example, Drayton and Primack (2000) found survival rates over 3 years from 0% to 5.8% for eight forest herb seed additions. Although our results confirm that *S. diphyllum* can emerge and survive when seeds are translocated, we need to measure long-term survival to confirm its ability to establish self-sustaining populations. The few studies that have tracked seed addition experiments over several years have found that the number of initially occupied patches with successful recruitment exponentially decreases over time (Drayton & Primack, 2012; Ehrlén et al., 2006).

Broad-scale habitat suitability did not predict seedling emergence rates or short-term seedling survival. This could be due to the failure of the SDMs to predict habitat suitability accurately because they may not always incorporate important predictors or their resolution may be too coarse to define fine-scale habitat heterogeneity relevant to seedling recruitment and survival (Fowler et al., 1981; Guisan & Thuiller, 2005; Maschinski et al., 2012). However, the predictions of the range-edge SDM were correlated with the presence and abundance of common wood-poppy associates (Results S1; Table S2; Figures S3 and S4) suggesting the range-edge SDM has some ability to differentiate habitat conditions. Alternatively, SDMs may effectively predict habitat suitability for long-term population viability but not for seedling emergence and short-term survival. Plant niche requirements can change with life stage (Grubb, 1977). The SDMs we used are based on conditions at existing occurrences dominated by adult plants, but the optimal conditions for germination can be different from those for establishment (Drayton & Primack, 2000; Eriksson, 2002). We will continue to monitor the translocated populations to determine if SDM-predicted habitat suitability can determine long-term viability.

Overall, the strongest predictor of seedling emergence was the presence or absence of seed predators. Emergence rates were 75% to 79% higher inside cages than in unprotected sub-plots. Bowles (2000) found that 90% of *S. diphyllum* seeds placed on experimental trays at one of the wild Ontario populations were removed within 24 h, confirmed as rodent activity through mice faeces containing *S. diphyllum* seed coats (COSEWIC, 2007). Our findings suggest that seed predation is severely limiting seedling emergence rates. *Stylophorum diphyllum* may be prone to elevated levels of seed predation in southern Ontario due to high levels of habitat fragmentation, which can lead to increased rodent density. For example, Tallmon et al. (2003) found that deer mice densities were three to four times higher and trillium seeds were about three times more likely to be removed in small forest fragments compared to continuous forests. Given these high levels of seed predation, translocation attempts must create or find 'safe sites' that are free of predators (e.g., Jeffries & Lawton, 1984; Jusaitis, 2005), and seed protection may be required at the existing populations to enable these populations to persist long term.

Although we designed the cages to exclude seed predators, we cannot discount the microclimatic effect of cages as an alternate or additional cause of differences in seedling emergence rates (Davis & Gedalof, 2018; Evans et al., 2018). Cages with smaller mesh sizes like ours can influence microclimate by providing a barrier against natural elements (e.g. snow and rain) or change in airflow, resulting in air and ground temperature differences that fluctuate based on other site factors such as canopy cover (Bergez & Dupraz, 2000; Evans et al., 2018). However, studies that have tested the microclimatic effects of cages have found that these effects are usually minor compared to the effect of predator exclusion (Brown & Vellend, 2014; Davis & Gedalof, 2018; Pearson et al., 2012). In addition, cages can influence untargeted biotic factors. We observed a thick accumulation of leaf litter outside cages compared to inside our closed-top cages. Leaf litter can reduce seedling emergence for buried seeds, acting as a mechanical barrier (Rotundo & Aguiar, 2005). Therefore, we cannot rule out litter reduction as a contributor to the cage effect we observed.

From a conservation standpoint, our findings suggest that we must take a more proactive approach to recover dispersal-limited species. Recovery strategies for plant species at risk in Canada (almost all of which occur near their northern range limit; Caissy et al., 2020) often focus solely on protecting existing populations under the assumption that occupied sites represent most of the available suitable habitat. For example, many recovery strategies define critical habitat for plants by drawing a buffer around existing populations (e.g. Environment and Climate Change Canada, 2014, 2017). However, our results emphasize the importance of dispersal limitation in combination with biotic factors in limiting the frequency of occurrence rather than the lack of suitable habitat (Tables 1 and 2; Figures 2 and 3). Conserving few, small, isolated populations is insufficient for species that require assisted dispersal to colonize new sites if increasing the number of populations is the goal (Primack, 1996; Primack & Miao, 1992). Isolation through anthropogenic habitat destruction and fragmentation exacerbates this situation, because when suitable patches become too isolated, dispersal between sites can no longer occur, leading to a functionally extinct metapopulation (Holt & Keitt, 2000; Hylander & Ehrlén, 2013). Assisted dispersal may be the best option for such species, especially those relying on a dispersal agent with limited capabilities, such as ants (typical dispersal disperse <10 m; Corlett, 2009).

Understanding the causes of species rarity is a fundamental goal of ecological theory that is necessary for the effective conservation of rare species. Our study simultaneously tested the role of dispersal, abiotic, and biotic factors on the emergence and survival of a rare plant species at its range edge. Theory emphasizes the scarcity of habitat with suitable abiotic conditions in limiting species occurrences near their range edge; however, we did not find broad-scale suitable habitat availability to be a limiting factor, at least for seedling emergence and short-term survival. Instead, we found that dispersal limitation coupled with biotic factors and microclimate had a greater relative influence. If other rare, dispersal-limited plant species at their range edge exhibit this pattern, their recovery will require assisted dispersal in combination with mitigation of negative biotic interactions to establish persistent populations.

AUTHOR CONTRIBUTIONS

Emma R. Neigel collected, curated and analysed the data, co-led project conceptualization and was the primary writing lead of the manuscript. J. L. McCune secured funding for the research, co-led project conceptualization, helped with data collection, advised on data analysis and supported writing and editing the manuscript. Timothy D. Schwinghammer advised on statistical analysis and performed the response surface regressions.

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CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are archived in the Federated Research Data Repository (FRDR): Neigel, E.R. & McCune, J.L. (2025). Experimental seed addition trials for the wood-poppy (*Stylophorum diphyllum*). Federated Research Data Repository (https://doi.org/10.20383/103.01247).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Dispersal limitation and seed predation drive rarity of a plant species at its range edge.

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