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Less is more: vegetation changes coincide with white-tailed deer suppression over thirty years

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Abstract

Although ecological impacts of overabundant white-tailed deer (*Odocoileus virginianus*) are well documented in eastern North America, few studies have evaluated the long-term effects of adaptive deer population suppression after a period of overabundance. We examined vegetation community changes over a period of 30 years (1992–2021) on the Long Point Peninsula, Ontario, Canada following a >85% reduction of a previously overabundant white-tailed deer population. We documented a significant increase in species diversity and shifts in the species composition of understory plants and woody vegetation. We then evaluated several hypotheses to explain these patterns. Our results provide support for the all-you-can-browse hypothesis, in which the abundance of woody stems above the browse layer did not increase within the first 3 years of sampling but, consistent within an expected period of recruitment, increased by >1,500% from 1995–2021. We also found support for both the lawn maintenance hypothesis, with a significant decline in the proportional abundance of non-preferred species relative to preferred species, and for the seed bank hypothesis, with native species accounting for nearly 80% of new species observed over the sampling period. We conclude that the effective, long-term management and continued suppression of an previously overabundant white-tailed deer population can lead to increased vegetation community heterogeneity and diversity, which is likely one of the most important steps for the regeneration of woody stems and native vegetation communities.

KEYWORDS
deer management, exotic species, Long Point, *Odocoileus virginianus*, overabundant deer, protected areas, vegetation regeneration

Moins c'est plus : les changements de végétation coïncident avec la suppression des cerfs de Virginie sur trente ans

Résumé

Bien que les impacts écologiques de la surabondance de cerfs de Virginie (*Odocoileus virginianus*) soient bien documentés dans l'est de l'Amérique du Nord, peu d'études ont évalué les effets à long terme de la suppression adaptative de la population de cerfs après une période de surabondance. Nous avons examiné les changements de la communauté végétale sur une période de 30 ans (1992–2021) dans la péninsule de Long Point, en Ontario, au Canada, à la suite d'une réduction de >85% d'une population auparavant surabondante de cerfs de Virginie. Nous avons documenté une augmentation significative de la diversité des espèces et des changements dans la composition spécifique des plantes du sous-étage et de la végétation ligneuse. Nous avons ensuite évalué plusieurs hypothèses pour expliquer ces tendances. Nos résultats sont conformes à une hypothèse de "brouter tout ce qui est a portée" car l'abondance des tiges ligneuses au-dessus de la couche de brout n'a pas augmenté au cours des 3 premières années d'échantillonnage mais, par la suite, pendant une période de recrutement prévue, a augmenté de >1,500% de 1995 à 2021. Nous avons également trouvé un soutien à une hypothèse "d'entretien de pelouses", car il y a eu une baisse significative de l'abondance proportionnelle des espèces non préférées par rapport aux espèces préférées. Une troisième hypothèse soulignant l'importance de la banque de semences est également soutenue dans la mesure où près de 80% des nouvelles espèces observées pendant la période d'échantillonnage étaient d'origine indigène. Nous concluons que la gestion efficace à long terme et la suppression continue d'une population auparavant surabondante de cerfs de Virginie peuvent conduire à une hétérogénéité et une diversité accrues des communautés végétales, ce qui constitue probablement l'une des étapes les plus importantes pour la régénération des tiges ligneuses et des communautés végétales d'origine.

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INTRODUCTION

Species in the family Cervidae (deer) are present on every continent across the globe except Antarctica (Tanentzap et al. 2012). As deer are the dominant herbivore in many ecosystems, the relationship between deer browse and ecological communities has been extensively evaluated at local and regional scales in parts of Africa (Dolman and Wäber 2008, Spear and Chown 2009), Asia (Takahashi and Kaji 2001, Takatsuki 2009), Australasia (Coomes et al. 2003, Moriarty 2004, Bee et al. 2009, Forsyth et al. 2010, Wright et al. 2012), Europe (Angelstam et al. 2000, Fløjgaard et al. 2017, Martin et al. 2018, Simončič et al. 2019), North America (Tanentzap et al. 2011, Nuttle et al. 2013, Schmit et al. 2020), and South America (Dolman and Wäber 2008). The introduction and re-introduction of deer have led to a widespread overabundance of both native and non-native deer species, augmented by changes in land uses, enhanced hunting regulations, widespread extirpation of predators, and an increase in refugia (Horsley et al. 2003, Long et al. 2007, Le Saout et al. 2014, Nuttle et al. 2014, Chollet et al. 2015). Most notably, a biologically overabundant deer population that exceeds the carrying capacity of an ecological system can cause the simplification of vegetation communities (Gill and Beardall 2001, Rooney and Waller 2003, Côté et al. 2004, Martin et al. 2011, Chollet et al. 2015), especially if their overabundance is prolonged over decades (Pendergast et al. 2016).

In North America, white-tailed deer (*Odocoileus virginianus*) populations have fluctuated drastically since the early seventeenth century (Russell et al. 2001), but contemporary population estimates suggest they are the most dominant wild herbivore in temperate forest regions (Myers et al. 2004). Prior to European colonization, white-tailed deer densities in North America were estimated to have ranged from 3.1–7.7 individuals/km^2 (McCabe and McCabe 1997, Horsley et al. 2003). However, by the mid-nineteenth century, overharvesting pressures on white-tailed deer led to widespread declines and regional extirpations across their North American range (Rooney 2001, Long et al. 2007, Bressette et al. 2012). Shortly after, extensive reintroduction efforts gave rise to white-tailed deer populations that became biologically overabundant, frequently at densities >7.7–14.0 individuals/km^2, which have generally continued to the present day (Côté et al. 2004, Long et al. 2007, Rushing et al. 2020). Where predators are absent and ample food resources and refugia exist, localized white-tailed deer populations have been recorded at densities >60 individuals/km^2 (Augustine and de Calesta 2003, Rushing et al. 2020, Schmit et al. 2020) and, in extreme cases, >110 individuals/km^2 (Rooney and Waller 2003). Contemporary deer populations often surpass an ecosystem's recommended carrying capacity, evident in 59% of forest communities that contain moderate or high browse impacts in the northeastern United States (McWilliams et al. 2018). Conversely, when white-tailed deer are suppressed to roughly 4.0–6.0 individuals/km^2 through active management interventions, continued regeneration of browse-sensitive vegetation species has occurred (Anderson 1994, Crimmins et al. 2010, Russell et al. 2017). Still, there has been limited testing of vegetation community regeneration during periods of deer population suppression at the landscape scale (Habeck and Schultz 2015).

Browsing by a biologically overabundant white-tailed deer population is known to have negative and far-reaching impacts on vegetation communities and the wider landscape (Jones et al. 1996, Côté et al. 2004, Baiser et al. 2008, Pendergast et al. 2016). Overabundant deer can suppress woody and herbaceous species regeneration within the browse layer (i.e., 0–2.0 m above the ground), and reduce recruitment of woody species above the browse layer (≥2.0 m; McShea and Rappole 2000, Rooney and Waller 2003, Melis et al. 2006). Further, browsing by overabundant deer can act as a disturbance regime that can increase the abundance and spread of exotic and invasive species (Myers et al. 2004, Vavra et al. 2007, Eschtruth and Battles 2008, Lesser et al. 2019), shift abiotic processes such as nutrient cycling (McNeil et al. 2005, Allombert et al. 2005*b*, Martin et al. 2010), and cause trophic cascade effects across vertebrate and invertebrate communities (Feber et al. 2001, Allombert et al. 2005*a*, Beguin et al. 2011, Nuttle et al. 2011, Bush et al. 2012, Cardinal et al. 2012, Frye 2012, Palmer et al. 2015). Moreover, white-tailed deer are selective browsers (Horsley et al. 2003, Rooney 2009, Russell et al. 2017), which disproportionately affect browse-sensitive vegetation (McShea and Rappole 2000, Parker et al. 2020). Browse-sensitive species such as wild lily-of-the-valley (*Maianthemum canadense*), eastern white cedar (*Thuja occidentalis*), and white trillium (*Trillium grandiflorum*) can be suppressed to the point of local extirpation (Augustine and Frelich 1998, Goetsch et al. 2011, Jenkins et al. 2014), although regeneration is possible if the species persists in a seed bank or re-establishes from a nearby source (Royo and Carson 2008). The subsequent loss of above-ground vegetation species can result in community homogenization in which non-preferred vegetation can dominate the understory (Rooney 2009, Tanentzap et al. 2009, Pendergast et al. 2016, Russell et al. 2017), which can, in turn, support the development of a recalcitrant layer; a persistent vegetation layer that is resistant to displacement (Royo and Carson 2006). A recalcitrant layer can restrict the regeneration of other vegetation (e.g., tree seedlings and saplings) within the browse layer to effectively limit recruitment above the browse layer (De La Cretaz and Kelty 2002, Tanentzap et al. 2011, Nuttle et al. 2013, Thomas-Van Gundy et al. 2014, Pendergast et al. 2016). Still, little is known about the regeneration of woody and browse-sensitive species, persistence of exotic species, or patterns of non-preferred species after a deer population has been suppressed for several decades.

Whether regeneration of vegetation occurs immediately or over decades following the reduction of an overabundant deer population, the period of study is critical for identifying the expected outcomes of deer management on vegetation communities in the long-term (McGarvey et al. 2013). Carson et al. (2005) stated that a lag period or legacy effect exists following the reduction of overabundant deer and termed this period the ghost of herbivory past. A legacy effect, defined as the persistence of a disturbance's impact even after the disturbance has been removed (Cuddington 2011, Nuttle et al. 2014, Pendergast et al. 2016), could continue for decades or centuries after deer reduction (Tanentzap et al. 2012, Bradshaw and Waller 2016, Blossey et al. 2019). In contrast to this supposition, Bernes et al. (2018) reported that control-impact studies related to deer population reduction or removal only lasted a median of 6 years. Short-term investigations can indeed provide important insights, but long-term studies (>20 years) are crucial for a robust understanding of trends of vegetation community regeneration (McGarvey et al. 2013, Bernes et al. 2018).

We used 2 long-term vegetation monitoring datasets sampled over a period of 30 years (1992–2021) to evaluate vegetation community changes on the Long Point Peninsula (hereafter referred to as Long Point) in Ontario, Canada following a >85% reduction of a previously overabundant white-tailed deer population. Control-impact studies at Long

Point conducted before vegetation monitoring began in 1991 identified a clear relationship between overabundant white-tailed deer and vegetation regeneration within fenced exclosure plots (McCullough and Robinson 1988). To address the lack of control plots, which previously existed at Long Point but were not maintained from 1991–2021, we first investigated general changes in the vegetation community composition, species richness, and diversity over 30 years at Long Point. Second, we examined several hypotheses to address how adaptive deer suppression from 1992–2021—that maintained white-tailed deer at a density of approximately <5 individuals/km^2—changed vegetation composition and species diversity.

For effects on vegetation composition, we tested predictions from 4 hypotheses (Table 1): 1) the all-you-can-browse hypothesis proposes that the browsing of palatable woody vegetation by overabundant deer prevents the recruitment of these species from the browse layer to the strata layer, 2) the selective deer browse hypothesis proposes that an overabundant deer population primarily prevents the recruitment of browse-sensitive species, such as white trillium (Anderson 1994), 3) the lawn maintenance hypothesis proposes that an overabundant deer population causes the development of an understory dominated by non-preferred species, such as grasses, because preferred species have been driven to extirpation, and 4) the disturbance competition hypothesis proposes that an overabundant deer population reduces competition for exotic species, resulting in an increase in their relative abundance and species richness. For effects on species diversity, we examined the seed bank hypothesis (Table 1), which proposes that the regeneration of species most expected following a period of high deer density will be native species, and that the proportion will be greater than exotic species. In this descriptive study, we detail each prediction and the measured variables for each of these hypotheses (Table 1). To examine these hypotheses, our analyses are based on the implicit assumption that the first part of the time series represents a period of white-tailed deer overabundance.

STUDY AREA

Long Point (42°35′N, 80°25′W) is the world's largest freshwater sandspit complex, located in rural Norfolk County in Ontario, Canada (Figure 1) at the northern extent of the Carolinian Zone (Almas and Conway 2016). The region sits approximately 200 m above sea level and has annual average temperatures between 19°C in summer months (June–September) and −3°C in winter months (December–March) with an average annual precipitation of 1,035.8 mm (Government of Canada 2023). Long Point is situated on the north shore of the central basin of Lake Erie and is a relatively new (~4,000 years old; Davidson-Arnott and Law 1990) and narrow sandspit (<6 km at its widest point) that comprises a total of 8,100 ha of sand dunes and wetlands extending 40.9 km eastward into Lake Erie from Long Point Creek, Ontario, Canada. Undulating sand ridges at Long Point sustain a complex sequence of ecologically diverse communities including open beaches, Great Lakes coastal meadow marshes, semi-open savannas, slough wetlands, coniferous lowlands, and mixed and deciduous-dominated upland woodlands and forests (McCracken et al. 1981, Reznicek and Catling 1989). Long Point is globally recognized as an area of ecological significance and has aptly been designated a World Biosphere Reserve (McCarthy et al. 2006), a Wetland of International Importance (Ramsar 2001), and an Important Bird Area (BirdLife International 2023).

Long Point has a history of both natural and anthropogenic disturbances with a well-documented written record of fire, extreme storm events, Great Lakes water level fluctuation, erosion, logging, invasion of exotic species, overhunting, reforestation and plantings, human development, and long-term occupation (>60 years) by an overabundant white-tailed deer population (Bradstreet 1977, Heffernan and Ralph 1978, McCracken et al. 1981). Other than the removal of a small number of locally exotic tree species (white poplar [*Populus alba*], Scots pine [*Pinus sylvestris*], and red pine [*Pinus resinosa*]), there was no active forest management during the study period.

Although white-tailed deer were extirpated from Long Point by 1870 (Snyder 1931; Figure 2), the Long Point Company, which owned the majority of Long Point as a private hunting club between 1866 and 1978, reintroduced

TABLE 1 A summary table of hypotheses and predictions associated with 2 key research questions regarding changes in vegetation in response to suppression of white-tailed deer from 1992–2021 at Long Point, Ontario, Canada.

Mechanism	Predictions	Response variable	References
Question 1	How did the composition of vegetation change on Long Point between 1992 and 2021?		
1) All-you-can-browse hypothesis			
Browsing of palatable woody vegetation by an overabundant white-tailed deer population prevents the recruitment of these palatable species from the browse layer into the strata above the browse layer.	a) There will be an increase in the abundance of all woody vegetation within the browse layer (0–2.0 m) over the study period.	Abundance of woody stems within the browse layer from 1992–2021.	Horsley et al. (2003), Royo et al. (2010), Schmit et al. (2020).
	b) There will be no change in the abundance of all woody vegetation above the browse layer (≥2.0 m) from 1992–1994, as an expected increase in stems ≥2.0 m will show a lag period following deer population reductions.	Abundance of woody stems above the browse layer from 1992–1994.	
	c) There will be an increase in the abundance of all woody vegetation above the browse layer (≥2.0 m) from 1995–2021 as stems are recruited.	Abundance of woody stems above the browse layer from 1995–2021.	
2) Selective deer browse hypothesis			
An overabundant white-tailed deer population prevents the recruitment of browse-sensitive species.	a) There will be an increase in the relative abundance of browse-sensitive woody species over time.	Proportion of browse-sensitive species abundance (compared to other non-sensitive woody species abundance).	Rooney (2009), Royo et al. (2010), Tremblay et al. (2006), Webster et al. (2005).
	b) There will be an increase in the relative abundance of browse-sensitive forb species over time.	Proportion of browse-sensitive forb abundance (compared to other non-sensitive forb species abundance).	
3) Lawn maintenance hypothesis			
An overabundant white-tailed deer population causes the development of an understory dominated by non-preferred species because preferred species have been driven to low abundance or local extirpation.	a) There will be a decline in the relative abundance of non-preferred species (i.e., grasses, ferns, and sedges) over time.	Proportion of non-preferred species (i.e., grasses, ferns, and sedges) abundance, as compared to all other preferred species (i.e., bryophytes, forbs, lichen, shrubs, trees, and vines) abundance.	Gubanyi et al. (2008), Rooney (2009), Tremblay et al. (2006), Trumbull et al. (1989).

TABLE 1 (Continued)

Mechanism	Predictions	Response variable	References
4) Disturbance competition hypothesis			
Browsing of native species by an overabundant white-tailed deer population reduces competition for exotic species, resulting in an increase in their relative abundance and species richness.	a) There will be a decrease in the relative abundance of exotic species over time.	Proportion of exotic species abundance (compared to native species abundance).	Knight et al. (2009), Aronson and Handel (2011), Vavra et al. (2007).
Question 2	How did the species diversity of vegetation increase on Long Point between 1992 and 2021?		
5) Seed bank hypothesis			
Browsing of vegetation by an overabundant white-tailed deer population causes local extirpation of above-ground vegetation species, but they can persist and regenerate via a sustained seed bank or source.	a) Of the new species detected, more will be native species than exotic species.	Proportion of the change in species richness of new native species (compared to new exotic species).	deCalesta (1994), DiTommaso et al. (2014), Horsley et al. (2003), Tremblay et al. (2006).

15 deer in 1874 (Long Point Company v. Anderson 1890). The population then grew rapidly because of a lack of predators and the enactment of stricter hunting regulations (Snyder 1931), which resulted in their prolonged overabundance between approximately 14–25 individuals/km^2 on Long Point for most of the twentieth century (McCullough and Robinson 1988; Figure 2). During this period of overabundance, deer had browsed all available vegetation within the browse layer (0–2.0 m above the ground), resulting in the development and maintenance of ecological communities that embodied park-like conditions (Snyder 1931).

After the establishment of the Long Point National Wildlife Area (NWA) in 1978 (McKeating 1983), the Canadian Wildlife Service (CWS) identified deer as the key disturbance of Long Point's vegetation communities and initiated monitoring and management actions for white-tailed deer on Long Point (Ashley et al. 1998). In 1988, the estimated density of white-tailed deer on Long Point was 22.7 individuals/km^2 (Figure 2) and, within the 8-km^2 deer wintering yard, was estimated to be 62.5 individuals/km^2 (McCullough and Robinson 1988). Shortly thereafter, CWS initiated lethal deer population culling efforts via public and managed hunts within the Long Point NWA (Lambert 1991, Sadler 2013). Between 1988 and 1991, culling eliminated >500 white-tailed deer, reducing the population by >85% (Bradstreet et al. 1992; Figure 2). Since 1991, monitoring of white-tailed deer by the CWS has continued in association with adaptive management efforts (i.e., lethal culling) to maintain the deer density at roughly <5 individuals/km^2 (Figure 2), as recommended by McCullough and Robinson (1988).

METHODS

The Long Point Bird Observatory and the CWS established a monitoring program in the spring of 1991 to evaluate the response of vegetation, insect, and breeding bird communities to deer population suppression (Bradstreet et al. 1992). Our study evaluates the woody stem and vegetation cover attributes that M. Bradstreet and others collected from 15 permanent monitoring sites between 1991 and 2021. Monitoring sites (Figure 1) ranged in size

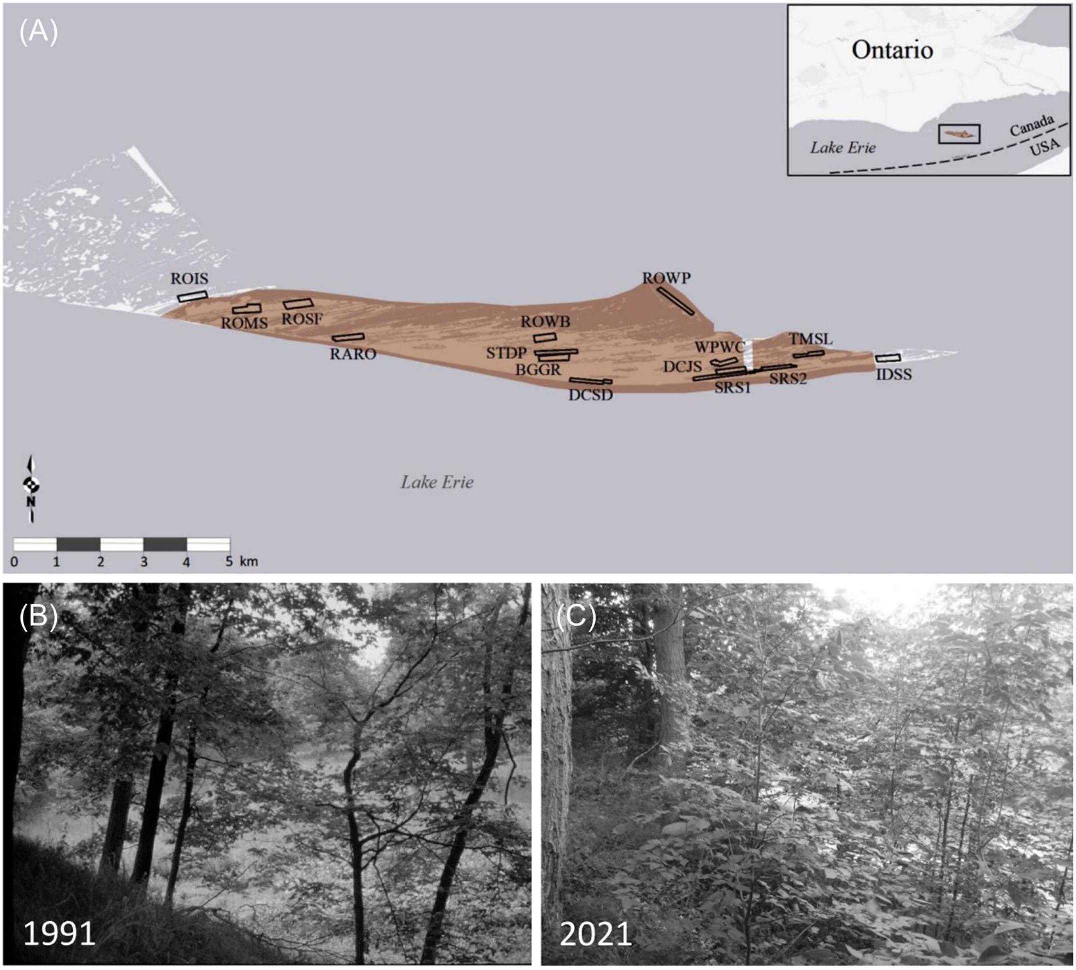

FIGURE 1 A) The study area and Long Point National Wildlife Area (shaded red) with the locations of 15 permanent monitoring sites located on the north shore of Lake Erie in southern Ontario (inset) at Long Point, Ontario, Canada. The location of each site is identified by a 4-letter code name, which corresponds to the vegetation community defined during the establishment of the Long Point Breeding Bird Census monitoring project in 1991 (Table A1; Bradstreet et al. 1992). Panel B) and C) show the view of understory regeneration from 1992–2021 at the ROMS monitoring site at Long Point, Ontario, Canada. Photographs were taken at the same location 30 years apart by Michael S. W. Bradstreet.

from 7.9–15.0 ha and were characterized and labeled according to qualitative descriptions of the dominant vegetation canopy species and community appearance (Bradstreet et al. 1992; Table A1). Each monitoring site was laid out in a rectangular grid arrangement with 50 × 50-m nested grid squares (~2,500 m^2; Figure A1). The southwest corner of each grid square was identified by its unique location within the rows (e.g., A–E) and columns (e.g., 1–20) of the grid, and demarcated in the field by a 5 × 5-cm wooden post with a labeled metal sign. Iron bars were paired with 10 of these wooden posts within each monitoring site to denote the locations of permanent vegetation sampling points.

All botanical nomenclature of species, including both scientific and common names reported herein, follow the provincial database for Ontario, Canada (Natural Heritage Information Centre 2021; Table A2). M. Bradstreet and others identified all sampled vegetation to the species level where possible or, in rare cases, recorded the genus or

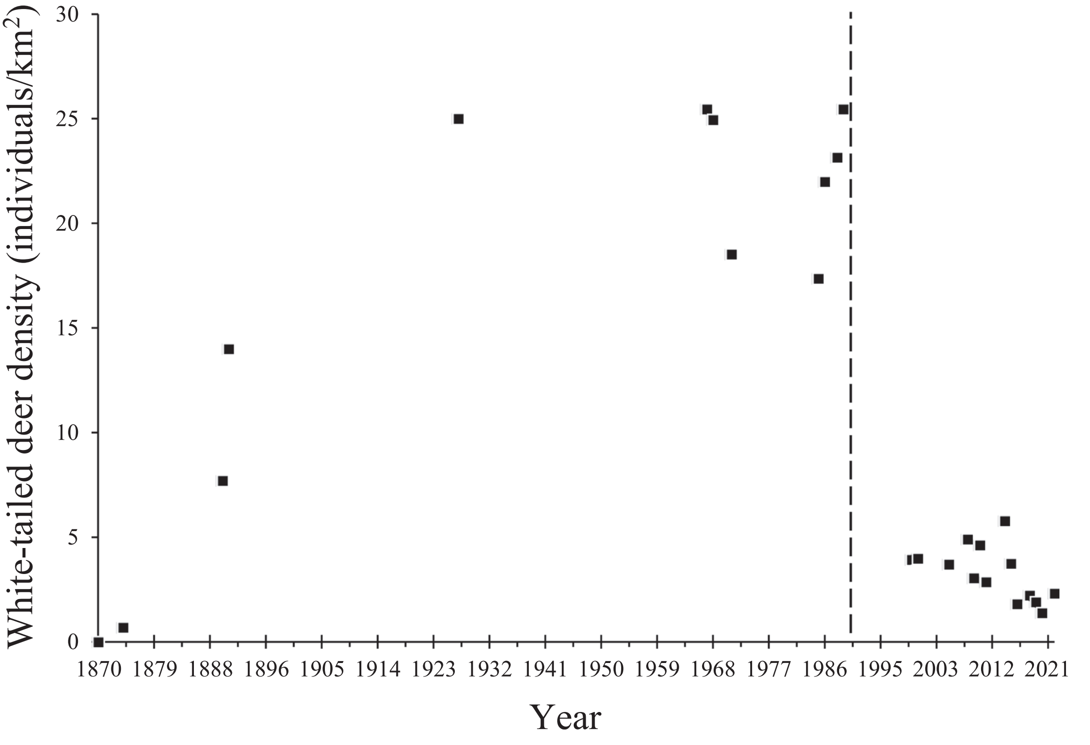

FIGURE 2 Compiled data of white-tailed deer population density estimates from 1870–2022 at Long Point, Ontario, Canada. The dashed vertical line represents the first year that active lethal white-tailed deer population suppression efforts began (i.e., Data sources: Bernard (2022), Bradstreet et al. (1992), McCullough and Robinson (1988), and Sadler (2013).

family when identification was unclear. Species sampled in the woody count dataset were organized into 4 growth forms: shrub, tree, vine, and unknown. Similarly, species sampled in the vegetation cover dataset were organized into 10 growth forms: bryophyte, fern, forb, grass, lichen, sedge, shrub, tree, vine, and unknown.

Woody stem counts and vegetation cover surveys

The woody count dataset consisted of the sum of woody stems (i.e., shrubs, trees, and vines) within a 10 × 1-m (10 m^2) quadrat at each of the 10 vegetation sampling points within each of the 15 monitoring sites from 1992–2021 (except for 2013 when monitoring could not be completed). Each 10-m^2 quadrat was oriented in a north-facing direction, delineated by the southwest-situated iron bar and a northwest-situated white polyvinyl chloride (PVC) pipe. During woody stem sampling, a 10-m rope was positioned between the iron bar and the PVC pipe to mark the western boundary of the quadrat, with the eastern boundary demarcated by a 1-m wooden dowel. Within each 10-m^2 quadrat, M. Bradstreet and others recorded the total count of all woody stems with a diameter at breast height (DBH) <7.5 cm and identified stems to species. They also assigned every sampled woody stem to 1 of 4 height categories: small (0 to ≤0.5 m), medium (>0.5 to ≤1.0 m), tall (>1.0 to <2.0 m), and very tall (≥2.0 m). In 2015, researchers first observed woody stems (e.g., tree seedlings) that measured ≥7.5 cm DBH within the defined height categories and, therefore, created a new category they termed saplings (Bradstreet 2016).

The vegetation cover dataset comprised estimates of proportional cover of all above-ground vegetation species (including woody stems) within a 1 × 1-m (1 m^2) quadrat at each of the 10 vegetation sampling points within each of the

15 monitoring sites from 1992–2012, and thereafter in 2017 and 2021. Each 1-m^2 quadrat was nested within the northern extent of the woody count quadrat (10 m^2) with white PVC pipes that were permanently installed in the northwest (same pipe as the woody count quadrat) and southeast corners of the 1-m^2 quadrat. During sampling, surveyors placed a collapsible 1-m^2 frame over the PVC pipes to identify the sampling area. A trained botanist assigned proportional cover codes for all species present within the sampling quadrat using the 5-point Braun Blanquet scale (Mueller-Dumbois and Ellenberg 1974). Cover codes (r, +, 1, 2, 3, 4, and 5) corresponded to a percent cover range: ≤0.1%, >0.1% to ≤1%, >1% to ≤5%, >5% to ≤25%, >25% to ≤50%, >50% to ≤75%, and >75%, respectively. Researchers then converted the defined cover range to a percentage midpoint: 0.01, 0.1, 2.5, 15, 37.5, 62.5, and 87.5 as a measure of the total cover for each species in each 1-m^2 quadrat.

Defining palatability and browse-sensitive species

To examine changes within and above the browse layer, we defined palatable woody vegetation as any woody stem species accessible to deer browse (i.e., within the browse layer). We considered all woody stems as palatable because previous study of deer browsing at Long Point demonstrated with experimental exclosure plots that virtually no woody plant growth was regenerating within the browse layer (McCullough and Robinson 1988). We considered woody stems in the small, medium, and tall categories (i.e., 0–2.0 m) as within the browse layer, and stems recorded in the very tall and sapling categories (i.e., ≥2.0 m) as above the browse layer. To evaluate the impacts on browse-sensitive species, we identified 6 species (Table A3) that have been shown to be disproportionately affected by overabundant deer browse in eastern North America: 4 woody species (eastern white pine [*Pinus strobus*], northern red oak [*Quercus rubra*], Allegheny blackberry [*Rubus allegheniensis*], and eastern white cedar) and 2 herbaceous forb species (wild lily-of-the-valley, and white trillium).

Statistical analyses

We performed all data analyses using R software version 4.1.2 (R Core Team 2021) with the vegan (Oksanen et al. 2022), glmm (Knudson 2022), and brms (Bürkner 2017, 2018, 2021) packages. The R code we used in analysis is available in Supporting Information.

To describe changes in vegetation community composition over time, we employed non-metric multidimensional scaling (NMDS) ordination with a Bray-Curtis dissimilarity distance value matrix (Bray and Curtis 1957). We fitted 12 NMDS models for the abundance of all species within the vegetation community for comparing 1992 to 6 additional years in the dataset (i.e., 1992 vs. 1997, 1992 vs. 2002, 1992 vs. 2007, 1992 vs. 2012, 1992 vs. 2017, and 1992 vs. 2021). We developed 6 models for the abundance of all species in the woody count dataset ($n = 40$) and another 6 models for all species in the vegetation cover dataset ($n = 271$). The NMDS models reduced the total abundance of all species to 2 axes, and we plotted each monitoring site within ordination space to visualize changes in community composition across time. To describe changes in species richness over time, we fitted a generalized linear mixed model (GLMM) with Poisson distribution for species richness of vegetation communities sampled from both the woody count and vegetation cover datasets from 1992–2021. For each GLMM, we included time (year) as a fixed effect, and the monitoring site and sampling quadrat as random effects. To describe changes in species diversity over time, we fitted 2-part hurdle models with binomial and gamma distributions to the Shannon index of diversity (Shannon 1948) for vegetation in both the woody count and vegetation cover datasets. For each 2-part hurdle model, we included time (year) as a fixed effect. Hurdle models employ 2 separate processes: a binomial distribution for binary responses of zero and a gamma distribution for positive non-zero values. Results of each hurdle model are plotted over time and an estimate is reported for the fixed effect. We used 95% upper and lower confidence intervals to evaluate whether the estimated year effect overlapped with zero.

To test the 3 predictions associated with the all-you-can-browse hypothesis, we fitted 3 GLMMs. For prediction 1a (Table 1), we fitted a GLMM for the abundance of woody stems within the browse layer from 1992–2021 and, for predictions 1b and 1c (Table 1), we fitted separate GLMMs for the abundance of woody stems above the browse layer from 1992–1994 and then from 1995–2021. For all models, we included time (year) as a fixed effect and monitoring site and sampling quadrat as random effects. Additionally, to describe the change in overall abundance of woody stems over the study period, we calculated the percent change in the abundance of woody stems both within and above the browse layer in 1992 and 2021.

To test prediction 2a (Table 1) of the selective deer browse hypothesis, we first calculated the proportion of the abundance of browse-sensitive woody stems (as compared to non-browse-sensitive woody stems) within each sampling quadrat from 1992–2021 and then fitted a zero-one-inflated augmented beta (ZOIB) regression distribution model with time (year) included as a fixed effect. We used the ZOIB distribution model because a high percentage of values were zero or one. The ZOIB models employ 2 separate processes: a Bernoulli distribution for binary responses of zero and one and a beta distribution for values between zero and one (Douma and Weedon 2019). All models included time (year) as a fixed effect, but random effects cannot be included in ZOIB models. We plotted results of ZOIB distribution models over time and reported the posterior mean estimate for the fixed effect. We assessed the time effects by examining whether the 95% upper and lower confidence intervals overlapped with zero. From ZOIB models, we calculated the posterior estimate of the fixed effect (year), precision or dispersion (ϕ), the zero-one-inflation probability (α), and the conditional one-inflation probability (γ). To test prediction 2b (Table 1), we first calculated, within each sampling quadrat for each year, the proportion of the abundance of browse-sensitive forbs relative to all forbs and, like above, used a ZOIB distribution model with time (year) as a fixed effect.

To test predictions from the lawn maintenance hypothesis (3a; Table 1) and disturbance competition hypothesis (4a; Table 1), we also used a ZOIB distribution model for each response variable, respectively: proportion of grasses to all other species and proportion of exotic species to all native species. To test prediction 5a (Table 1) from the seed bank hypothesis, we compared the increase of new native species, which are expected to regenerate from the seed bank or nearby source, with the increase of new exotic species. We also described changes to the total count of new species sampled from the vegetation cover dataset over the study period.

RESULTS

Change in vegetation community composition, species richness, and diversity over time

The NMDS ordination of the woody count dataset showed very little change within the first 5 years of sampling (i.e., 1992–1997) with less overlap of vegetation communities in 2002, 2007, 2012, 2017, and 2021 when compared to 1992 (Figure 3). The smaller hull size of the 2021 woody stem community indicates monitoring sites are becoming more similar to each other than those in 1992 for woody stem composition (Figure 3). The woody stem community after 1992 showed a greater association with species known to benefit from deer exclusion including red ash (*Fraxinus pennsylvanica*), and eastern white cedar (Bradshaw and Waller 2016, Jenkins and Howard 2021). In the NMDS analysis of the vegetation cover dataset (Figure 4), the composition was also slow to change within the first 5 sampling years (i.e., 1992–1997). By 2021 the vegetation cover hull expanded relative to 1992, suggesting monitoring sites are becoming less similar to each other over time for vegetation cover composition (Figure 4).

Overall, species richness and diversity (Shannon index of diversity) of vegetation communities from the woody count and vegetation cover datasets increased over the 30-year period (Figure 5). Results from GLMMs supported a linear increase in species richness within the woody count dataset ($\beta = 0.634 \pm 0.082$ [SE], $P < 0.001$; Table B1) and the vegetation cover dataset ($\beta = 0.087 \pm 0.044$, $P = 0.05$; Table B2). Similarly, results from 2-part hurdle models

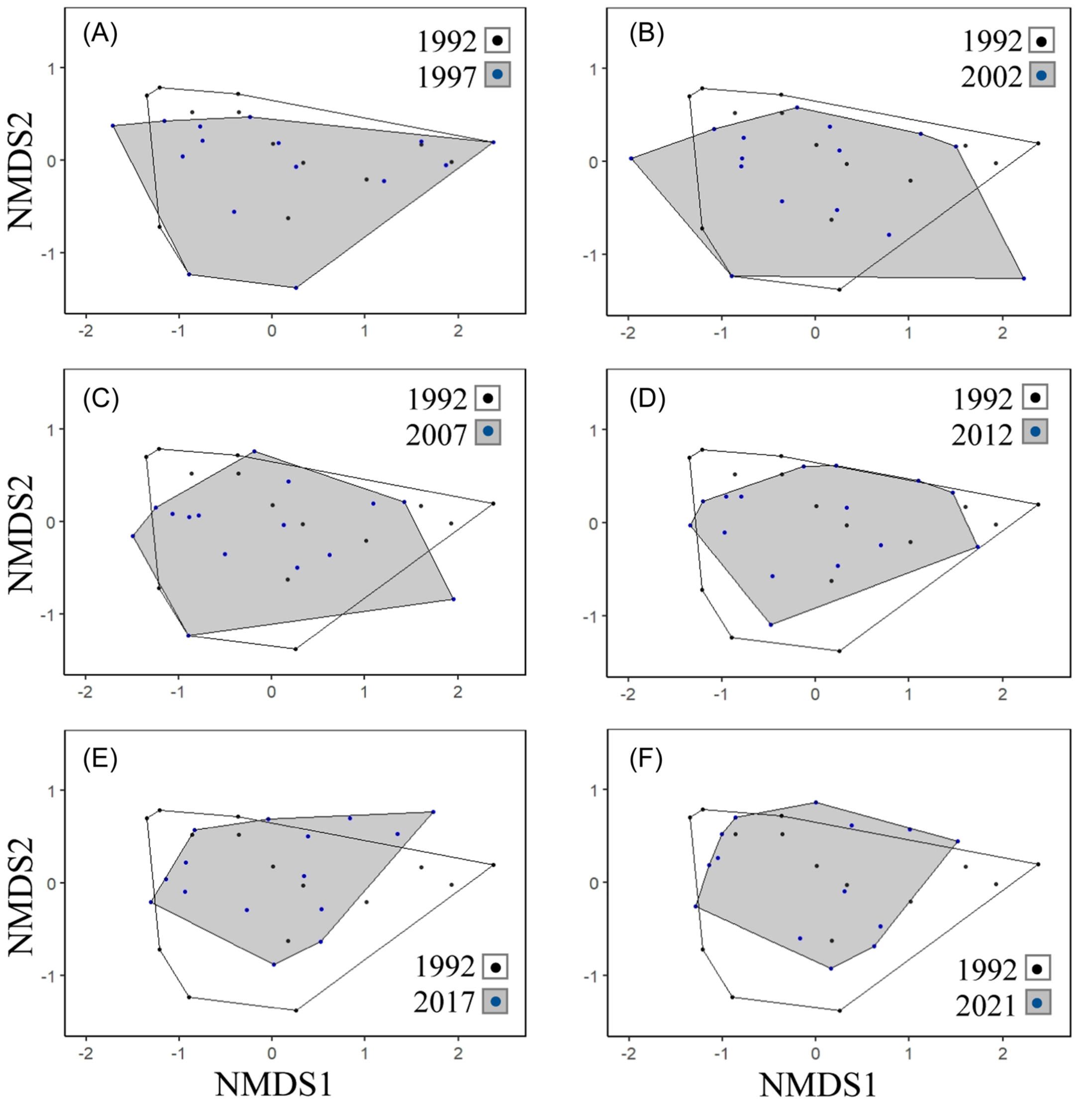

FIGURE 3 Ordination plots of all species sampled from the woody count dataset comparing communities between 1992 and 6 temporal snapshots in A) 1997, B) 2002, C) 2007, D) 2012, E) 2017, and F) 2021 at Long Point, Ontario, Canada. Each species sampled was distributed in non-metric multi dimensional scaling (NMDS) ordination space for each monitoring site for the 6 periods.

supported a linear increase in species diversity within the woody count dataset (Table 2; Figure B1) and the vegetation cover dataset (Table 3; Figure B2) from 1992–2021.

Prediction testing

Analysis of woody stems over time provided mixed support for the all-you-can-browse hypothesis. Contrary to prediction 1a (Table 1), there was no support for a linear increase in the abundance of woody stems within the browse layer over the study period ($\beta = -0.009 \pm 0.018$, $P = 0.60$; Figure 6; Table B3). However, consistent with

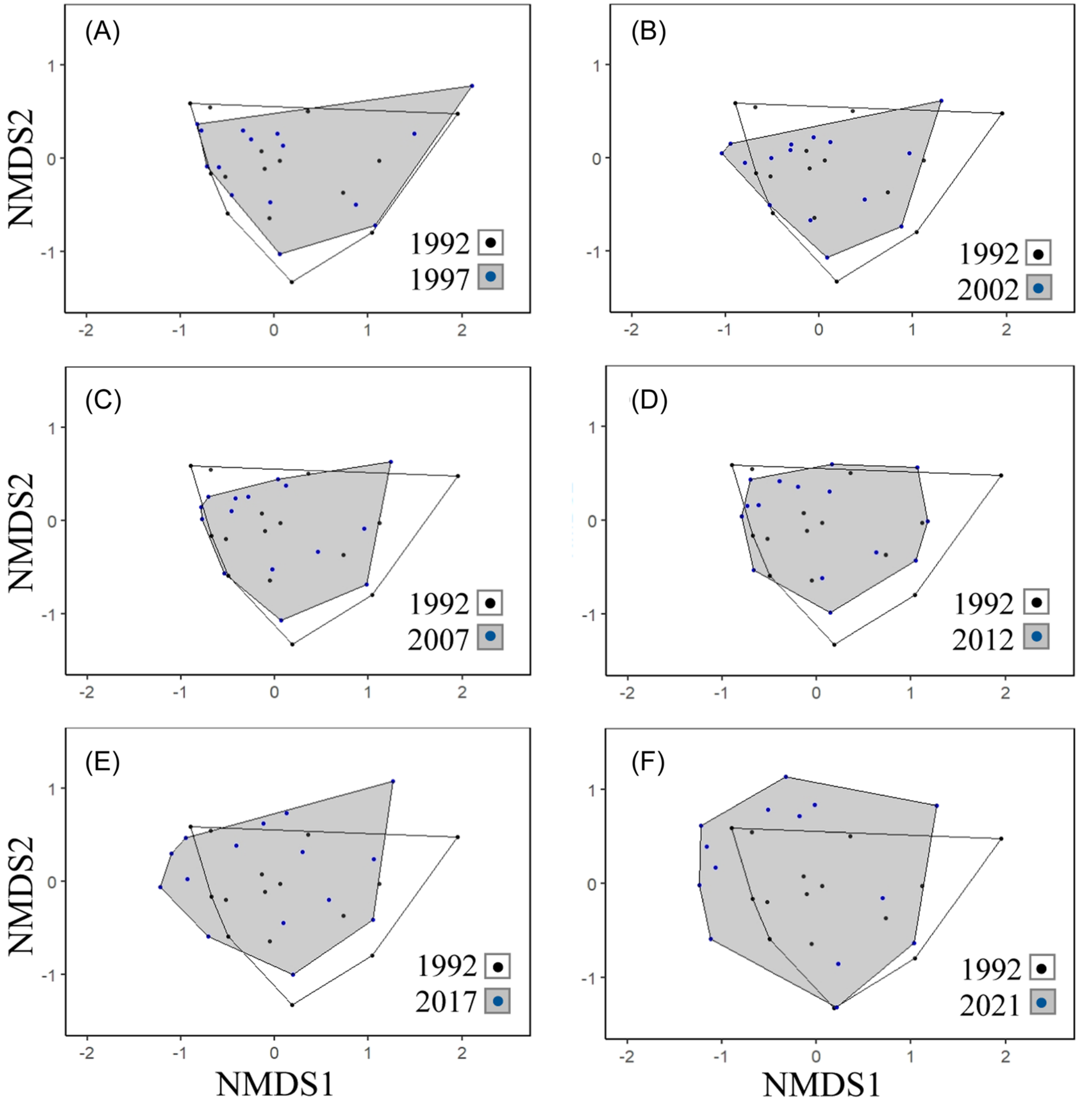

FIGURE 4 Ordination plots of all species sampled from the vegetation cover dataset comparing communities between 1992 and 6 temporal snapshots in A) 1997, B) 2002, C) 2007, D) 2012, E) 2017, and F) 2021 at Long Point, Ontario, Canada. Each species sampled was distributed in non-metric multi dimensional scaling (NMDS) ordination space for each monitoring site for the 6 periods.

predictions 1b and 1c (Table 1), there was no evidence for an increase in woody stems above the browse layer from 1992–1994 ($\beta = -0.096 \pm 0.398$, $P = 0.81$; Table B4) but strong evidence for an increase thereafter ($\beta = 1.828 \pm 0.186$, $P < 0.001$; Figure 6; Table B5). Results showed that between 1992–1994 the abundance of woody stems above the browse layer declined 8% but between 1995–2021 increased >1,500%.

We found no support for the selective deer browse hypothesis. In contrast to prediction 2a (Table 1), there was no evidence for an increase in the proportion of browse-sensitive woody stems (as compared to non-browse-sensitive woody stems) over the study period (Table 4; Figure C1). Similarly, results did not support prediction 2b (Table 1), as there was no evidence for an increase in the proportion of browse-sensitive forbs (as compared to non-sensitive forbs) from 1992–2021 (Table 5; Figure C2). In support of the latter result, white trillium, a known

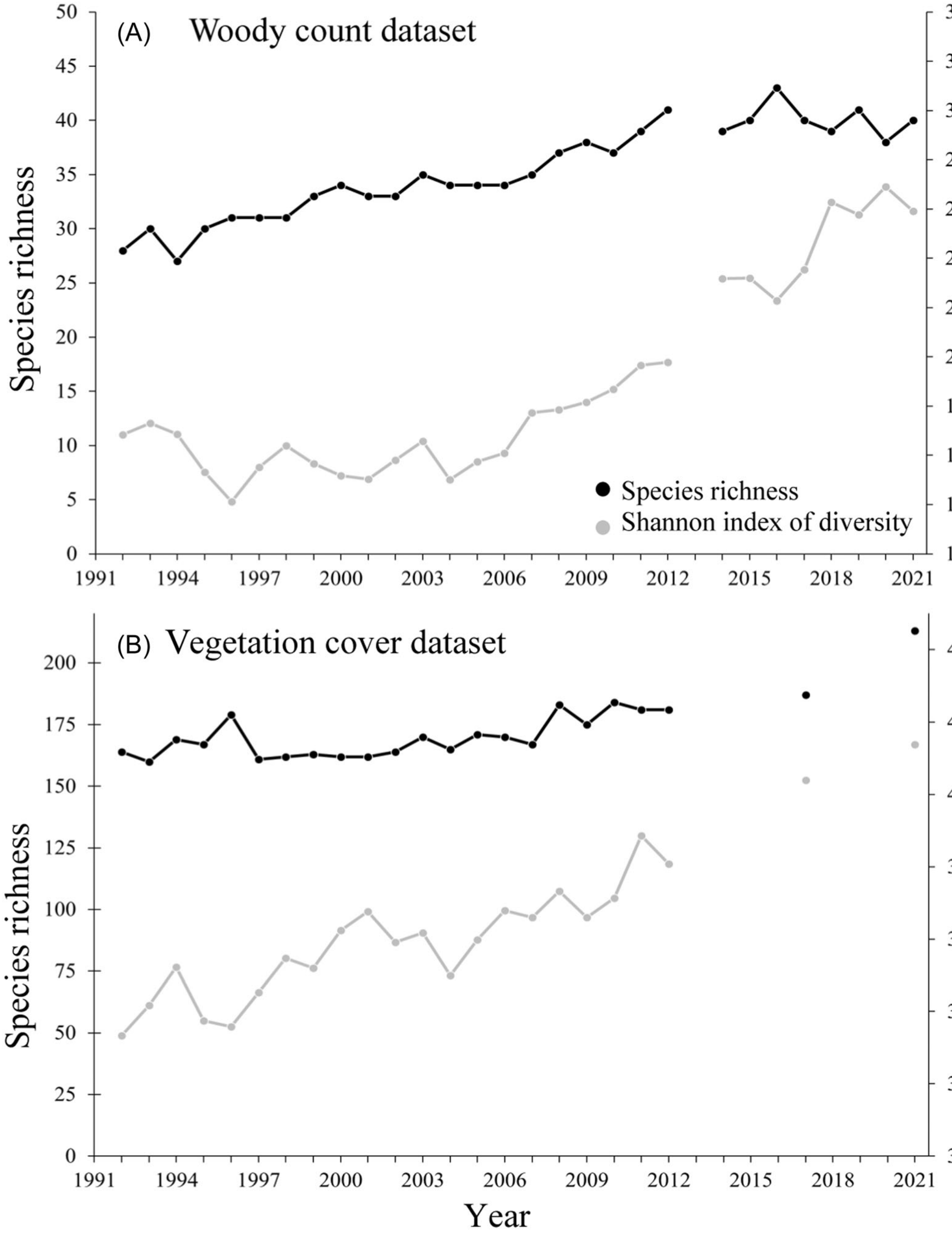

FIGURE 5 Scatterplot showing the change in the annual sum of species richness and the Shannon index of diversity from vegetation communities sampled from the A) woody count dataset, and B) vegetation cover dataset within all monitoring sites from 1992–2021, at Long Point, Ontario, Canada.

indicator of deer browse effects (Rooney and Gross 2003), was absent from most sampling years and was only recorded at one monitoring site during the entire study.

We found support for the lawn maintenance hypothesis. Consistent with prediction 3a (Table 1), the proportion of non-preferred species types (i.e., grasses, ferns, and sedges) relative to other species types (i.e., bryophytes,

TABLE 2 Summary results of a 2-part hurdle model to explain variation in vegetation species diversity (Shannon index of diversity) from the woody count dataset (n = 3,439, df = 3,438) collected from 1992–2021 at Long Point, Ontario, Canada, with year (i.e., 1992–2021) as a fixed effect. The woody count dataset consisted of the sum of woody stems (i.e., shrubs, trees, and vines) within a 10 × 1-m (10 m^2) quadrat at each of the 10 vegetation sampling points within each of the 15 monitoring sites from 1992–2021 (except for 2013 when monitoring could not be completed).

Term[a]	β ± SE	Lower 95% CI	Upper 95% CI
Intercept	−32.82 ± 3.25	−39.22	−26.59
Year	0.02 ± 0.00	0.01	0.02
Hu	0.25 ± 0.01	0.24	0.27

[a]Term included for quadrats with zero counts for the Shannon index of diversity (Hu).

TABLE 3 Summary results of 2-part hurdle model to explain variation in vegetation species diversity (Shannon index of diversity) from the vegetation dataset (n = 3,375, df = 3,374) collected from 1992–2021 at Long Point, Ontario, Canada, with year (i.e., 1992–2021) as a fixed effect. The vegetation cover dataset comprised estimates of proportional cover of all above-ground vegetation species (including woody stems) within a 1 × 1-m (1 m^2) quadrat at each of the 10 vegetation sampling points within each of the 15 monitoring sites from 1992–2012, and thereafter in 2017 and 2021.

Term[a]	β ± SE	Lower 95% CI	Upper 95% CI
Intercept	−12.91 ± 2.88	−18.34	−7.32
Year	0.01 ± 0.00	0.00	0.01
Hu	0.03 ± 0.00	0.02	0.04

[a]Term included for quadrats with zero counts for the Shannon index of diversity (Hu).

forbs, lichen, shrubs, trees, and vines) declined over time (Table 6; Figure 7 and C3). Supporting this pattern, the 3 most abundant non-preferred species sampled in 1992, bluejoint reedgrass (*Calamagrostis canadensis*), Canada bluegrass (*Poa compressa*), and Kentucky bluegrass (*Poa pratensis*), declined by 71%, 65%, and 97%, respectively, when compared to the last year of monitoring in 2021.

We also found strong support for the disturbance competition hypothesis. Consistent with prediction 4a (Table 1), the proportional abundance of exotic species over native species declined over time (Table 7; Figure C4). Supporting these model results, the total abundance of exotic species declined by 49% between the first and last sampling year, while native species increased 28% in the same period (Figure 8). Furthermore, 3 of the most abundant exotic species at the beginning of the sampling period, leafy spurge (*Euphorbia virgata*), common St. John's-wort (*Hypericum perforatum*), and bittersweet nightshade (*Solanum dulcamara*), declined by 100%, 93%, and 68%, respectively, when compared to the last sampling year. However, not all exotic species followed the same pattern; European reed (*Phragmites australis* ssp. *australis*), which was nearly absent in 1992 (0.1% cover), increased by approximately 500,000% between 1992 and 2021, and was the most abundant exotic species by 2021. Another exotic species, multiflora rose (*Rosa multiflora*), was not observed in any monitoring site within the first 4 sampling years but increased to 56 stems by 2021, suggesting variation in the relationships between some exotic species and white-tailed deer suppression.

Consistent with prediction 5a (Table 1) of the seed bank hypothesis, 78% (n = 187) of the 239 new species observed since 1992 were classified as native (Table D1). The remaining species were classified as exotic (17%, n = 41) or of unknown status (5%, n = 11), suggesting that the increase in new species was primarily driven by an increase in native species.

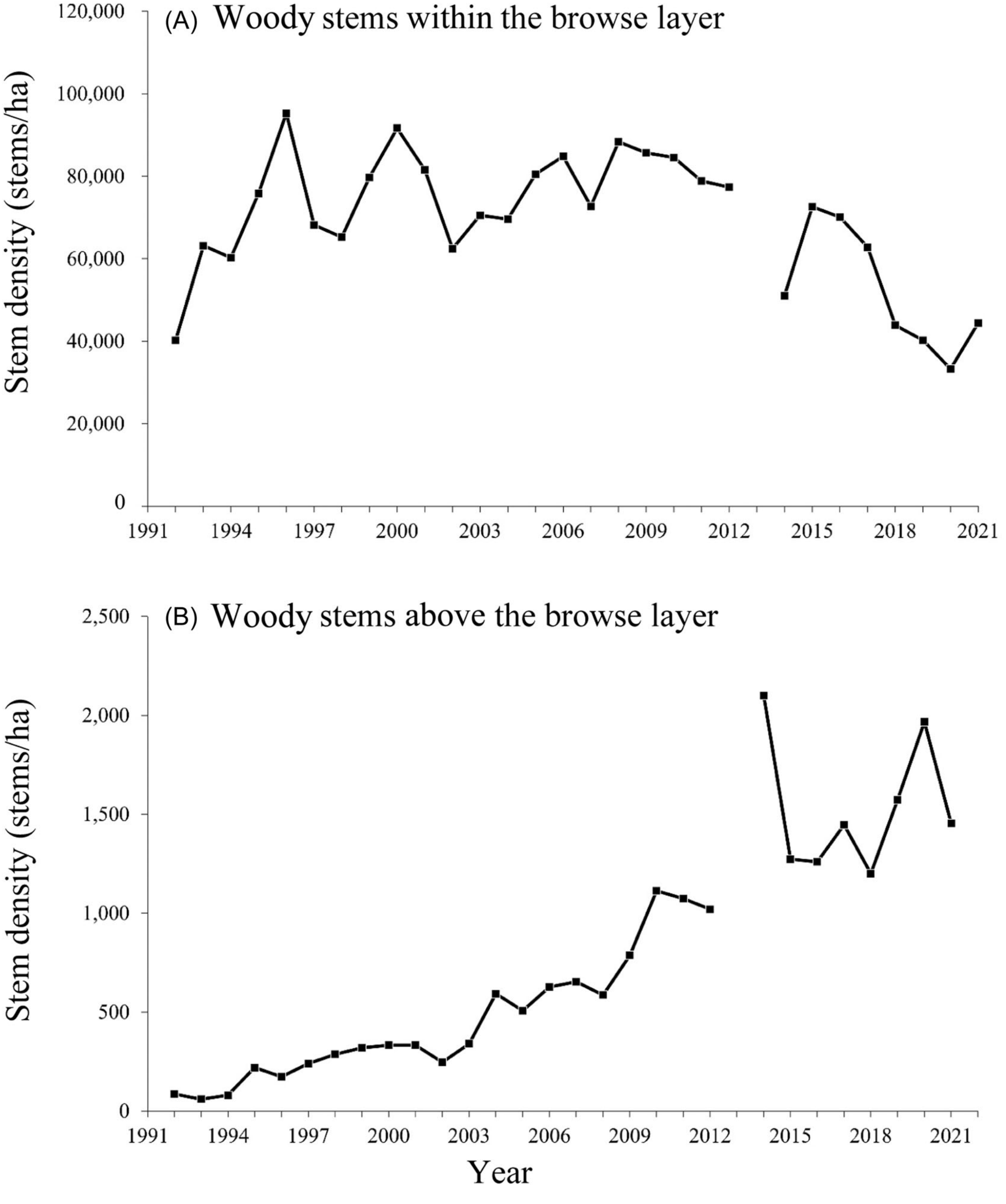

FIGURE 6 Scatterplot showing the change in A) the abundance of woody stems within the browse layer (0–2.0 m) and B) the abundance of woody stems above the browse layer (≥2.0 m) sampled at all monitoring sites from 1992–2021 at Long Point, Ontario, Canada.

DISCUSSION

During a period of adaptive deer suppression from 1992–2021 that maintained the white-tailed deer population at a density of roughly <5 individuals/km^2, we show that the vegetation communities sampled at Long Point, Ontario, Canada underwent a significant shift in both their composition and diversity. Although changes in the composition

TABLE 4 Summary of results from a zero-one-inflated beta regression model to explain changes in the proportional abundance of browse-sensitive woody stems (compared to non-browse-sensitive woody stems) from the woody count dataset (n = 3,439, df = 3,438) collected from 1992–2021 at Long Point, Ontario, Canada, with year (i.e., 1992–2021) as a fixed effect. The woody count dataset consisted of the sum of woody stems (i.e., shrubs, trees, and vines) within a 10 × 1-m (10 m^2) quadrat at each of the 10 vegetation sampling points within each of the 15 monitoring sites from 1992–2021 (except for 2013 when monitoring could not be completed).

Term[a]	β ± SE	Lower 95% CI	Upper 95% CI
Intercept	−8.49 ± 11.28	−30.86	13.69
ϕ intercept	−30.68 ± 11.72	−54.15	−8.25
α intercept	107.22 ± 9.82	88.31	126.78
γ intercept	199.06 ± 80.26	53.49	365.73
Year	0.00 ± 0.01	−0.01	0.01
ϕ year	0.02 ± 0.01	0.00	0.03
α year	−0.05 ± 0.00	−0.06	−0.04
γ year	−0.10 ± 0.04	−0.19	−0.03

[a]Terms included a year effect, a precision or dispersion parameter (ϕ), the zero-one-inflation probability (α), and the conditional one-inflation probability (γ).

TABLE 5 Summary of results from a zero-one-inflated beta regression model to explain changes in the proportional abundance of browse-sensitive forb species (compared to non-browse-sensitive forb species) from the vegetation cover dataset (n = 2,957, df = 2,956) collected from 1992–2021 at Long Point, Ontario, Canada, with year (i.e., 1992–2021) as a fixed effect. The vegetation cover dataset comprised estimates of proportional cover of all above-ground vegetation species (including woody stems) within a 1 × 1-m (1 m^2) quadrat at each of the 10 vegetation sampling points within each of the 15 monitoring sites from 1992–2012, and thereafter in 2017 and 2021.

Term[a]	β ± SE	Lower 95% CI	Upper 95% CI
Intercept	50.37 ± 52.02	−49.06	149.92
ϕ intercept	−8.08 ± 43.31	−92.41	78.72
α intercept	132.04 ± 35.11	62.66	199.51
γ intercept	−88.55 ± 200.43	−473.60	333.81
Year	−0.03 ± 0.03	−0.07	0.02
ϕ year	0.00 ± 0.02	−0.04	0.05
α year	−0.06 ± 0.02	−0.10	−0.03
γ year	−0.04 ± 0.10	−0.17	0.23

[a]Terms included a year effect, a precision or dispersion parameter (ϕ), the zero-one-inflation probability (α), and the conditional one-inflation probability (γ).

of vegetation communities at Long Point over the study period are likely the result of complex and potentially additive anthropogenic and natural disturbances locally, we discuss our results in the context of hypotheses relevant to deer-driven disturbance at the landscape scale. We also acknowledge that human-driven climate change may have magnified or diminished linear patterns of vegetation regeneration over the study period given that the Lake Erie basin has undergone drastic changes in average annual water levels, precipitation, and water temperature during the study period (Gronewold et al. 2013). Although local or regional climate modeling was not included in

TABLE 6 Summary of results from a zero-one-inflated beta regression model to explain changes in the proportional abundance of non-preferred species (i.e., grasses, ferns, and sedges), as compared to all other preferred species (i.e., bryophytes, forbs, lichen, shrubs, trees, and vines), from the vegetation cover dataset (*n* = 3,375, df = 3,374) collected from 1992–2021 at Long Point, Ontario, Canada, with year (i.e., 1992–2021) as a fixed effect. The vegetation cover dataset comprised estimates of proportional cover of all above-ground vegetation species (including woody stems) within a 1 × 1-m (1 m^2) quadrat at each of the 10 vegetation sampling points within each of the 15 monitoring sites from 1992–2012, and thereafter in 2017 and 2021.

Term[a]	β ± SE	Lower 95% CI	Upper 95% CI
Intercept	54.96 ± 6.62	43.50	66.61
ϕ intercept	−8.59 ± 5.06	−18.66	1.13
α intercept	6.17 ± 15.81	−24.66	38.08
γ intercept	125.05 ± 28.95	68.58	182.58
Year	−0.03 ± 0.00	−0.03	−0.02
ϕ year	0.00 ± 0.00	−0.00	0.01
α year	−0.00 ± 0.01	−0.02	0.01
γ year	−0.06 ± 0.01	−0.09	−0.03

[a]Terms included a year effect, a precision or dispersion parameter (ϕ), the zero-one-inflation probability (α), and the conditional one-inflation probability (γ).

this study, we suggest future research and vegetation community change modeling should consider complex additive or competition modeling frameworks to identify unknown relative impacts.

Woody stem recruitment

While we found only partial support for the all-you-can-browse hypothesis, we speculate that for prediction 1a, the absence of an effect within the browse layer was likely due to a methodological limitation of the sampling period rather than a biological explanation. In support of prediction 1b and 1c (Table 1), we found no evidence for an increase in woody stem recruitment above the browse layer during the first 3 years of sampling (1992–1994) but a dramatic increase in recruitment thereafter (1995–2021), particularly beginning in the mid-2000s (Figure 6). This finding is consistent with previous studies that have shown a lag period in woody species recruitment after a decline in overabundant deer (Tanentzap et al. 2011, Jenkins et al. 2015).

Prior to deer suppression, a local exclosure study at Long Point from the 1980s showed an increase in woody stem height between 1984 and 1986 in 2 plots where deer were excluded (McCullough and Robinson 1988). However, somewhat unexpectedly, and contrary to prediction 1a (Table 1), we found no evidence of an overall increase in the number of woody stems within the browse layer from 1992–2021. We suspect this is because the intervening period between the first large-scale deer reduction (1989) and the beginning of sampling (1992) may have been long enough to allow significant regeneration of woody stems within the browse layer. In support of this hypothesis, despite reports of virtually no woody stems during the earlier period of deer overabundance (McCullough and Robinson 1988), there were already approximately 40,000 woody stems/ha within the browse layer at the beginning of sampling in 1992 (Figure 6). Given that the abundance of woody stems more than doubled in the first 5 years of sampling (1992–1997; Figure 6) and based on growth described by McCullough and Robinson (1988), there was likely enough regeneration before sampling began in 1992 to sufficiently dampen any significant result that could have otherwise been detected from our analysis.

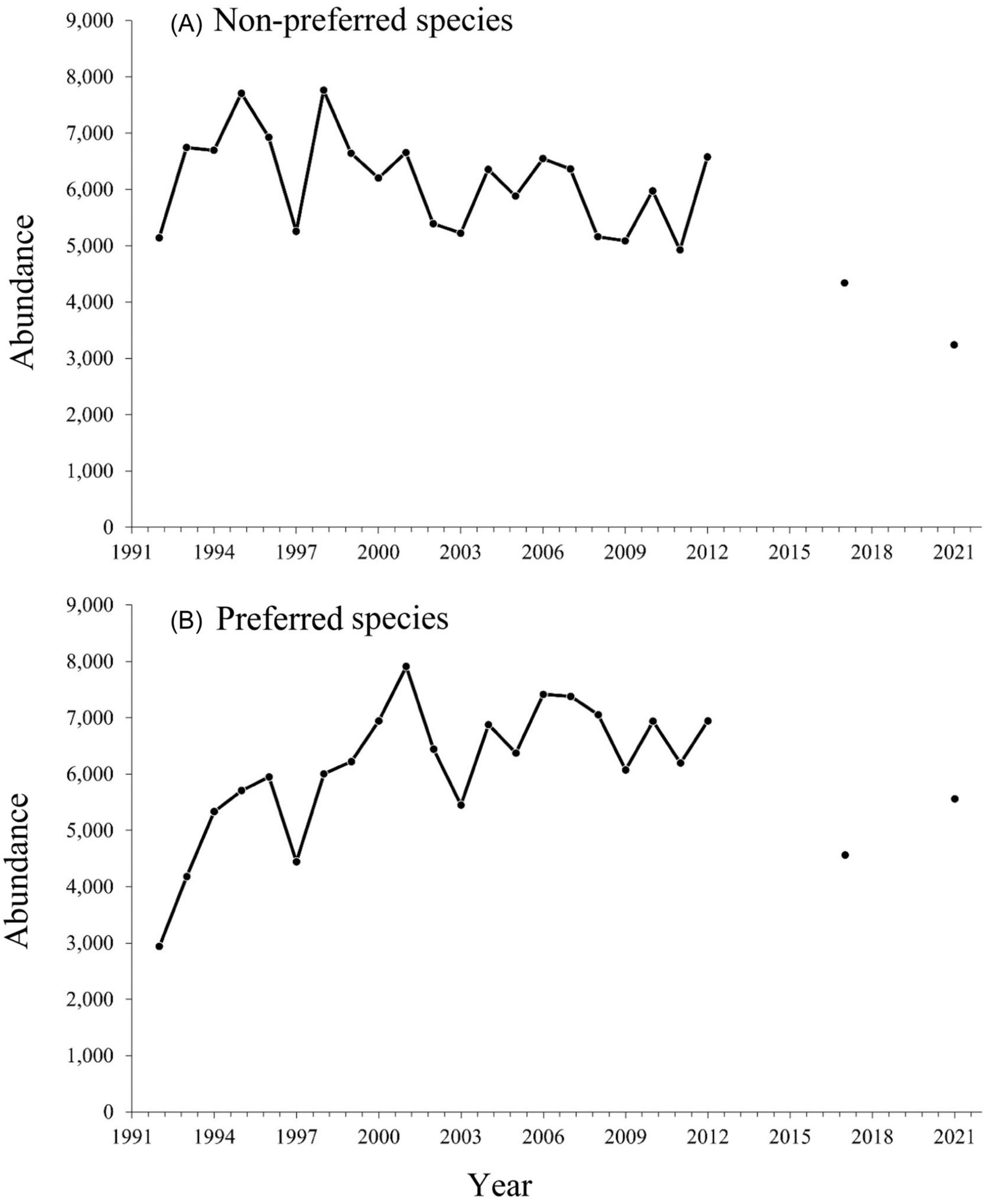

FIGURE 7 Scatterplot showing the change in A) the abundance of non-preferred species (i.e., grasses, ferns, and sedges) and B) the abundance of preferred species (i.e., bryophytes, forbs, lichen, shrubs, trees, and vines) sampled at all monitoring sites from the vegetation cover dataset from 1992–2021 at Long Point, Ontario, Canada.

Not all plants are equal: browse-sensitive and preferred species

Unlike our interpretation of the results as a sampling limitation for the all-you-can-browse hypothesis, we found little support for the selective deer browse hypothesis and suspect that a biological explanation was responsible.

TABLE 7 Summary of results from a zero-one-inflated beta regression model to explain changes in the proportional abundance of exotic species (compared to native species) from the vegetation cover dataset (n = 3,375, df = 3,374) collected from 1992–2021 at Long Point, Ontario, Canada, with year (i.e., 1992–2021) as a fixed effect. The vegetation cover dataset comprised estimates of proportional cover of all above-ground vegetation species (including woody stems) within a 1 × 1-m (1 m^2) quadrat at each of the 10 vegetation sampling points within each of the 15 monitoring sites from 1992–2012, and thereafter in 2017 and 2021.

Term[a]	β ± SE	Lower 95% CI	Upper 95% CI
Intercept	54.91 ± 6.94	41.39	68.58
ϕ intercept	−3.39 ± 6.12	−15.43	8.53
α intercept	4.17 ± 9.98	−14.90	23.20
γ intercept	−45.65 ± 98.38	−229.26	152.25
Year	−0.03 ± 0.00	−0.03	−0.02
ϕ year	0.00 ± 0.00	−0.00	0.01
α year	−0.00 ± 0.00	−0.01	0.01
γ year	0.02 ± 0.05	−0.08	0.11

[a]Terms included a year effect, a precision or dispersion parameter (ϕ), the zero-one-inflation probability (α), and the conditional one-inflation probability (γ).

The proportion of browse-sensitive woody and forb species as compared to non-browse-sensitive woody and forb species did not increase over the study period (Figures C1 and C2). The most parsimonious explanation for this lack of increase is that the suppressed deer population became more selective of their forage, as has been reported by others (Augustine and McNaughton 1998, Jenkins et al. 2015). Prior to deer suppression, there was evidence that the overabundant white-tailed deer population at Long Point was browsing species that are typically avoided as forage, such as eastern red cedar (*Juniperus virginiana*; Figure D1). However, although the deer population at Long Point was kept at relatively low densities (<~5 individuals/km^2) during the study period, browse-sensitive vegetation species (Table A3) were likely sought after as forage, which influenced their abundance because of shifts in the availability of forage species (Anderson 1994). Results from this study are consistent with others that indicate effective restoration of ecosystems previously affected by deer may require additional complementary management techniques beyond the efforts to suppress deer (Royo et al. 2010, Tanentzap et al. 2011, Nuttle et al. 2014). Such approaches may be as straightforward as supplemental plantings of browse-sensitive species (Royo et al. 2010) or as complex as prescribed burns or predator reintroductions (Tanentzap et al. 2011).

Our results suggest that the well-documented homogenization of vegetation communities dominated by non-preferred grasses, ferns, and sedges during periods of deer overabundance (Wright et al. 2019, Parker et al. 2020) can, to a degree, be reversed with long-term deer suppression. In support of the lawn maintenance hypothesis, from 1992–2021, we found that the proportional abundance of grasses, ferns, and sedges, as compared to preferred species, declined from 64% to 37%. Many areas changed from park-like conditions to areas dominated by a thick understory (Figure 1B, C). We suspect the most likely reason for such shifts in the understory is that, in the absence of overabundant deer, non-preferred species associated with lawn conditions lost their competitive advantage over other preferred species, including fast-growing woody stems that pushed out those non-preferred species. An exception to this pattern amongst non-preferred forms appears to be ferns, which suggests there may be alternative stable states of non-preferred species occurring and shows some support for the theory of multiple system states created by deer browse (Stromayer and Warren 1997). While grasses and sedges declined during the study period by 50% and 43%, respectively, ferns increased by 25%, dominated by a surge in fern allies, such as horesetails (*Equisetum* spp.).

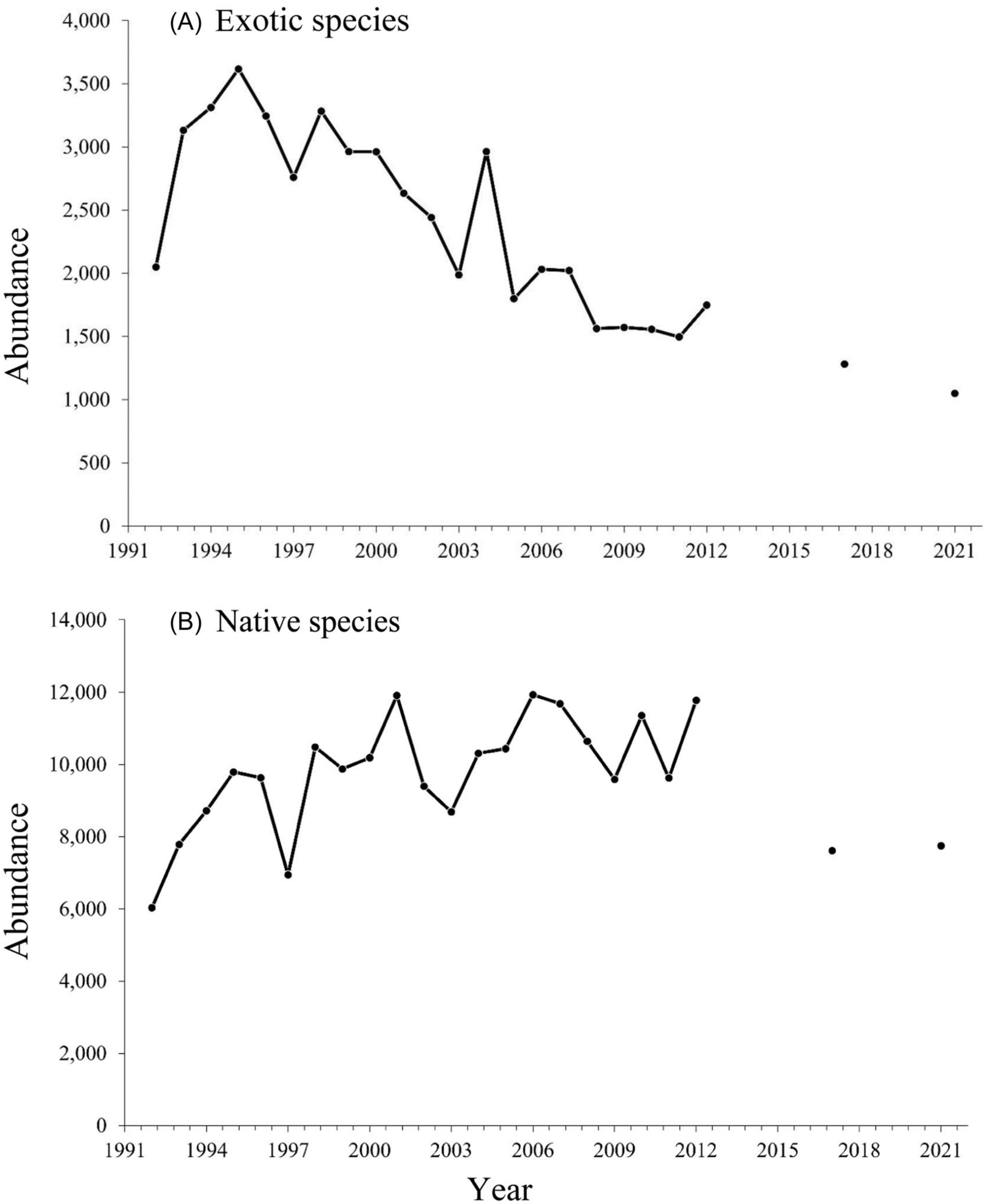

FIGURE 8 Scatterplot showing the change in A) the abundance of exotic species and B) the abundance of native species sampled at all monitoring sites from the vegetation cover dataset from 1992–2021 at Long Point, Ontario, Canada.

Results coincide with findings by Rooney (2009) who reported increases in ferns both inside and outside deer exclusion plots in Wisconsin, USA, indicating effects other than deer abundance and preference, such as shade tolerance and difference in reproduction strategies of ferns compared to grasses and sedges (Horsley et al. 2003), are likely responsible for such changes.

Exotic and native species

Similar to the decline in non-preferred species, a significant decline in the abundance of exotic species demonstrated that an overabundant deer disturbance regime, which can promote the invasion and persistence of exotic species (Averill et al. 2017), may be reversed when deer are suppressed. We found strong support for the disturbance competition hypothesis; the proportional abundance of exotic species declined from 25% in 1992 to 12% in 2021. However, drastic increases in the abundance of individual exotic species over the study period, including European reed (~500,000%), suggests that not all exotic species respond similarly to deer population suppression. A recent study at Long Point by Jung et al. (2017) reported that the local increase in European reed is related to water level fluctuations, indicating that other ecosystem disturbances coinciding with deer suppression can produce varied and complex interactions for exotic species composition. Furthermore, an absence followed by an increase in the stem count of multiflora rose over the study period supports findings by Averill et al. (2017), who reported some exotic species, such as multiflora rose, directly benefit from deer population reductions. Our results indicate that vegetation communities are still subject to exotic species invasion and persistence even after the disturbance of deer overabundance has been reduced, signifying that additional support for invasive species management is warranted even as overall exotic species counts declined drastically during the study period.

Our results provide evidence that native species, which are preferred by deer compared to many exotic species (Averill et al. 2017), were the driver of the increase in new species observed after 1992. In support of the seed bank hypothesis, after 1992 there were 187 new native species recorded, suggesting that a period of deer suppression allowed the regeneration of native species from the seed bank or from a nearby source to occur (Horsley et al. 2003, Levine et al. 2012). While the composition and presence of some species within seed banks can be altered or removed altogether by overabundant deer (DiTommaso et al. 2014), our results clearly show that native species have regenerated during a period of deer suppression. Further, Chollet et al. (2016) reported that seed propagation was not a limitation of native species regeneration following a release from overabundant deer browse, suggesting that additional complex disturbances at Long Point may have magnified or diminished patterns of vegetation regeneration during the study period. There were also many new exotic species (41 species) recorded after 1992, demonstrating that there are likely introductions of species from sources beyond the local seed bank at Long Point. As a result of a continued invasion of new exotic species, even with native species increase, results herein support recommendations by Gorchov et al. (2021) that advocate exotic species management should be paired with deer suppression to promote further native species regeneration.

CONSERVATION IMPLICATIONS

Our results suggest that effective management and maintenance of abundant white-tailed deer populations in eastern North America is an important step for the regeneration of woody stems above the browse layer and native vegetation communities. The overall increase in species richness and diversity suggests conservation managers need to continue adaptive management efforts to maintain white-tailed deer at <5 individuals/km^2. Analyses revealed temporal variation in the woody count and vegetation cover datasets, especially with regards to slow regeneration within the first 5 years of sampling (i.e., 1992–1997). Our results also suggest that deer suppression efforts on their own are too simplistic for supporting vegetation community regeneration of browse-sensitive species and management of exotic species. As both active and passive ecological restoration efforts gain traction in the twenty-first century (Aronson et al. 2020, McDonald and Clarkson 2020), conservation managers should continue to reduce overabundant deer populations as one critical aspect of ecological restoration, while pairing population suppression with other allied restorative activities (Aronson et al. 2017, 2020). This may be especially true within protected areas, including those at Long Point, that act as a refuge for biodiversity and at-risk species.

ACKNOWLEDGMENTS

Following the release of 94 Calls to Action by the Truth and Reconciliation Commission of Canada (2015), we find it appropriate to first and foremost acknowledge that the study area, the Long Point Peninsula, is located on the treaty lands and territory of the Mississaugas of the Credit First Nation and within the traditional territories of the Neutral and Haudenosaunee Peoples. We would like to thank Birds Canada (formerly the Long Point Bird Observatory), and the Canadian Wildlife Service for their foresight in initiating and funding the Long Point Breeding Bird Census project in 1991 and their continued dedication to long-term ecological monitoring. We would also like to thank the Weston Family Foundation, the Nature Conservancy of Canada, and the Mitacs Accelerate Fellowship program for supplementary funding. Many significant contributions have been made by those who have collected, organized, and made data accessible as part of the long-term monitoring project at Long Point. Specifically, we would like to thank P. Ashley, D. Bernard, T. Bradstreet, G. Bryan, P. Burke, J. Carson, P. Carson, A. Darwin, P. Deacon, A. Dean, S. Dobbyn, J. Elchyshyn, M. Gartshore, G. Grabas, A. Hanson, R. Holmes, K. Jones, A. Kettle, L. King-Goddard, M. Jackson, B. Korol, A. Lachance, J. Lounds, C. Landon, G. McCullough, M. McFarlane, E. McRae, G. Mitchell, L. Paton, E. Pelz, J. Read, T. Reznicek, M. Richardson, R. Ridout, J. Robinson, J. Soetemans, and R. White for their time and effort. We would also like to acknowledge the late Dr. J. Bowles, for her many years of dedicated work as a principal researcher on the Long Point Breeding Bird Census project from 1991–2012. We also thank D. Strickland for the translation of our written abstract from English to French.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This research was conducted with permission from Environment and Climate Change Canada under a No-Fee End-Use Restricted License Agreement. No required ethical approval was obtained for this research project.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.23826741, https://doi.org/10.6084/m9.figshare.23826744, and https://doi.org/10.6084/m9.figshare.23826747.

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SUPPORTING INFORMATION

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

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APPENDIX A: MONITORING SITES AND SPECIES OBSERVED

TABLE A1 Attributes and descriptions of the 15 permanent monitoring sites sampled during vegetation monitoring from 1992–2021 at Long Point, Ontario, Canada.

Site code	Site name	Site location (latitude [N]/longitude [W])	Site size (ha)
BGGR	Blue grass grassland	42°32′48.607″/80°9′33.819″	13.7
DCJS	Dry cottonwood-juniper savanna	42°32′36.426″/80°6′50.662″	11.3
DCSD	Dry cottonwood sand dune	42°32′25.681″/80°9′20.044″	10.2
IDSS	Integrating dune swale savanna	42°32′48.073″/80°3′41.985″	10.9
SRS1	Sedge-rush swale 1	42°32′28.028″/80°7′12.967″	13.1
SRS2	Sedge-rush swale 2	42°32′30.7″/80°6′48.347″	9.2
STDP	Sedge tamarack dune pond	42°32′54.432″/80°9′48.381″	12.5
TMSL	Tamarack slough	42°32′54.497″/80°5′3.962″	7.9
WPWC	White pine-white cedar savanna	42°32′45.503″/80°6′33.649″	8.9
RARO	Red ash-red oak savanna	42°33′9.197″/80°13′12.356″	11.4
ROIS	Red oak-ironwood savanna	42°33′51.513″/80°16′18.239″	13.6
ROMS	Red oak-sugar maple savanna	42°33′41.131″/80°14′56.245″	14.6
ROMF	Red oak-sugar maple forest	42°33′46.613″/80°14′28.491″	15.0
ROWB	Red oak-white birch savanna	42°33′7.795″/80°9′59.517″	11.0
ROWP	Red oak-white pine savanna	42°33′38.441″/80°7′22.475″	12.8

TABLE A2 List of vegetation species sampled during vegetation monitoring from 1992–2021 at Long Point, Ontario, Canada.

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Acer rubrum	Red maple	ACERUBR	Tree	Native	B
Acer saccharum	Sugar maple	ACESACC	Tree	Native	B
Achillea millefolium	Common yarrow	ACHMILL	Forb	Exotic	VC
Agalinis purpurea	Purple false foxglove	AGAPURP	Forb	Native	VC
Ageratina altissima	White snakeroot	EUPRUGO	Forb	Native	VC
Agrostis gigantea	Redtop	AGRGIGA	Grass	Exotic	VC
Agrostis stolonifera	Creeping bentgrass	AGRSTOL	Grass	Exotic	VC
Anemone sp.	Anemone species	ANEMON	Forb	Native	VC
Anemone virginiana	Tall anemone	ANEVIRG	Forb	Native	VC
Apios americana	American groundnut	APIAMER	Forb	Native	VC

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Apocynum androsaemifolium	Spreading dogbane	APOANDR	Forb	Native	VC
Apocynum cannabinum	Hemp dogbane	APOCANN	Forb	Native	VC
Apocynum sp.	n/a	APOCYN	Forb	Native	VC
Arabidopsis lyrata	Lyre-leaved rockcress	ARALYRA	Forb	Native	VC
Arabidopsis thaliana	Mouse-ear cress	ARATHAL	Forb	Exotic	VC
Aralia hispida	Bristly sarsaparilla	ARAHISP	Shrub	Native	WC
Arctostaphylos uva-ursi	Common bearberry	ARCUVA	Shrub	Native	B
Arenaria serpyllifolia	Thyme-leaved sandwort	ARESERP	Forb	Exotic	VC
Aronia melanocarpa	Black chokeberry	AROMELA	Shrub	Native	WC
Artemisia campestris	Field wormwood	ARTCAMP	Forb	Native	VC
Asclepias incarnata	Swamp milkweed	ASCINCA	Forb	Native	VC
Asclepias syriaca	Common milkweed	ASCSYRI	Forb	Native	VC
Asplenium platyneuron	Ebony spleenwort	ASPPLAT	Fern	Native	VC
Barbarea vulgaris	Bitter wintercress	BARVULG	Forb	Exotic	VC
Berberis thunbergii	Japanese barberry	BERTHUN	Shrub	Exotic	B
Betula papyrifera	Paper birch	BETPAPY	Tree	Native	B
Bidens beckii	Water beggarticks	MEGBECK	Forb	Native	VC
Bidens cernua	Nodding beggarticks	BIDCERN	Forb	Native	VC
Bidens frondosa	Devil's beggarticks	BIDFRON	Forb	Native	VC
Bidens sp.	n/a	BIDENS	Forb	Native	VC
Bidens trichosperma	Crowned beggarticks	BIDCORO	Forb	Native	VC
Boehmeria cylindrica	Small-spike false nettle	BOECYLI	Forb	Native	VC
Bolboschoenus fluviatilis	River bulrush	SCIFLUV	Sedge	Native	VC
Borodinia canadensis	Canada rockcress	ARACANA	Forb	Native	VC
Borodinia laevigata	Smooth rockcress	ARALAEV	Forb	Native	VC
Brasenia schreberi	Watershield	BRASCHR	Forb	Native	VC
Bromus sp.	Brome species	BROMUS	Grass	n/a	VC
Cakile edentula	American sea rocket	CAKEDEN	Forb	Native	VC
Calamagrostis breviligulata	American beachgrass	AMMBREV	Grass	Native	VC
Calamagrostis canadensis	Bluejoint reedgrass	CALCANA	Grass	Native	VC
Calopogon tuberosus	Tuberous grass pink	CALTUBE	Forb	Native	VC
Calystegia sepium	Hedge false bindweed	CALSEPI	Forb	Native	VC
Campanula rotundifolia	Harebell	CAMROTU	Forb	Native	VC

(Continues)

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Cardamine pensylvanica	Pennsylvania bittercress	CRDPENS	Forb	Native	VC
Carex alata	Broad-winged sedge	CARALAT	Sedge	Native	VC
Carex albursina	White bear sedge	CARALBU	Sedge	Native	VC
Carex aquatilis	Water sedge	CARAQUA	Sedge	Native	VC
Carex aurea	Golden sedge	CARAURE	Sedge	Native	VC
Carex bebbii	Bebb's sedge	CARBEBB	Sedge	Native	VC
Carex blanda	Woodland sedge	CARBLAN	Sedge	Native	VC
Carex buxbaumii	Buxbaum's sedge	CARBUXB	Sedge	Native	VC
Carex cephaloidea	Thin-leaved sedge	CARCEPD	Sedge	Native	VC
Carex cephalophora	Oval-leaved sedge	CARCEPH	Sedge	Native	VC
Carex comosa	Bearded sedge	CARCOMO	Sedge	Native	VC
Carex crawfordii	Crawford's sedge	CARCRAW	Sedge	Native	VC
Carex cristatella	Crested sedge	CARCRIS	Sedge	Native	VC
Carex diandra	Lesser panicled sedge	CARDIAN	Sedge	Native	VC
Carex eburnea	Bristle-leaved sedge	CAREBUR	Sedge	Native	VC
Carex flava	Yellow sedge	CARFLAV	Sedge	Native	VC
Carex foenea	Bronze sedge	CARFOEN	Sedge	Native	VC
Carex garberi	Garber's sedge	CARGARB	Sedge	Native	VC
Carex gracillima	Graceful sedge	CARGRAC	Sedge	Native	VC
Carex granularis	Limestone meadow sedge	CARGRAN	Sedge	Native	VC
Carex hirsutella	Hairy green sedge	CARHIRS	Forb	Native	VC
Carex hystericina	Porcupine sedge	CARHYST	Sedge	Native	VC
Carex interior	Inland sedge	CARINTE	Sedge	Native	VC
Carex lacustris	Lake sedge	CARLACU	Sedge	Native	VC
Carex lasiocarpa	Woolly-fruit sedge	CARLASI	Sedge	Native	VC
Carex laxiculmis var. *copulata*	Bright-green spreading sedge	CARXCOP	Sedge	Native	VC
Carex leptalea	Bristle-stalked sedge	CARLEPT	Sedge	Native	VC
Carex molesta	Troublesome sedge	CARMOLE	Sedge	Native	VC
Carex muehlenbergii	Muhlenberg's sedge	CARMUEH	Sedge	Native	VC
Carex pedunculata	Long-stalked sedge	CARPEDU	Sedge	Native	VC
Carex pellita	Woolly sedge	CARLANU	Sedge	Native	VC
Carex pensylvanica	Pennsylvania sedge	CARPENS	Sedge	Native	VC
Carex prairea	Prairie sedge	CARPRAI	Sedge	Native	VC

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Carex praticola	Northern meadow sedge	CARPRAT	Forb	Native	VC
Carex pseudocyperus	Cyperus-like sedge	CARPSEU	Sedge	Native	VC
Carex radiata	Eastern star sedge	CARRADI	Sedge	Native	VC
Carex rosea	Rosy sedge	CARROSE	Sedge	Native	VC
Carex sp.	Sedge species	CAREX	Sedge	Native	VC
Carex stipata	Awl-fruited sedge	CARSTIP	Sedge	Native	VC
Carex stricta	Tussock sedge	CARSTRI	Sedge	Native	VC
Carex utriculata	Northern beaked sedge	CARUTRI	Sedge	Native	VC
Carex viridula	Greenish sedge	CARVIRI	Sedge	Native	VC
Carya ovata	Shagbark hickory	CAROVAT	Tree	Native	WC
Castilleja coccinea	Scarlet paintbrush	CASCOCC	Forb	Native	VC
Celastrus scandens	Climbing bittersweet	CELSCAN	Vine	Native	B
Celtis occidentalis	Common hackberry	CELOCCI	Tree	Native	B
Cephalanthus occidentalis	Eastern buttonbush	CEPOCCI	Shrub	Native	B
Cerastium arvense	Field chickweed	CERARVE	Forb	Native	VC
Cerastium fontanum	Common mouse-ear chickweed	CERFONT	Forb	Exotic	VC
Ceratophyllum demersum	Common hornwort	CERDEME	Forb	Native	VC
Cercis canadensis	Eastern redbud	CERCANA	Tree	Native	B
Chara sp.	n/a	CHARA	Forb	Native	VC
Chelidonium majus	Greater celandine	CHEMAJU	Forb	Exotic	VC
Chenopodium album	Common lamb's-quarters	CHEALBU	Forb	Exotic	VC
Cicuta bulbifera	Bulbous water-hemlock	CICBULB	Forb	Native	VC
Cicuta maculata	Spotted water-hemlock	CICMACU	Forb	Native	VC
Circaea canadensis	Broad-leaved enchanter's nightshade	CIRLUTE	Forb	Native	VC
Cirsium arvense	Canada thistle	CIRARVE	Forb	Exotic	VC
Cirsium muticum	Swamp thistle	CIRMUTI	Forb	Native	VC
Cirsium sp.	n/a	CIRSIU	Forb	n/a	VC
Cirsium vulgare	Bull thistle	CIRVULG	Forb	Exotic	VC
Cladium mariscoides	Smooth twig-rush	CLAMARI	Sedge	Native	VC
Clinopodium vulgare	Wild basil	CLIVULG	Forb	Native	VC
Comandra umbellata	Bastard toadflax	COMUMBE	Forb	Native	VC
Comarum palustre	Marsh cinquefoil	POTPALU	Forb	Native	VC
Conopholis americana	American cancerroot	CONAMER	Forb	Native	VC

(Continues)

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Convolvulus arvensis	Field bindweed	CONARVE	Forb	Exotic	VC
Corispermum americanum	American bugseed	CORHYSS	Forb	Native	VC
Cornus obliqua	Silky dogwood	CORAMOM	Shrub	Native	B
Cornus sericea	Red-osier dogwood	CORSTOL	Shrub	Native	B
Corylus americana	American hazelnut	CORAMER	Shrub	Native	WC
Cystopteris fragilis	Fragile fern	CYSFRAG	Fern	Native	VC
Cystopteris tenuis	Mackay's brittle fern	CYSTENU	Fern	Native	VC
Dactylis glomerata	Orchard grass	DACGLOM	Grass	Exotic	VC
Danthonia spicata	Poverty oatgrass	DANSPIC	Grass	Native	VC
Decodon verticillatus	Swamp loosestrife	DECVERT	Shrub	Native	B
Dichanthelium implicatum	Slender-stemmed panicgrass	PANIMPL	Grass	Native	VC
Dichanthelium oligosanthes	Few-flowered panicgrass	PANOLIG	Grass	Native	VC
Dipsacus fullonum	Common teasel	DIPFULL	Forb	Exotic	VC
Dryopteris carthusiana	Spinulose wood fern	DRYCART	Fern	Native	VC
Dryopteris cristata	Crested wood fern	DRYCRIS	Fern	Native	VC
Dryopteris intermedia	Evergreen wood fern	DRYINTE	Fern	Native	VC
Dulichium arundinaceum	Three-way sedge	DULARUN	Sedge	Native	VC
Eleocharis acicularis	Needle spikerush	ELEACIC	Sedge	Native	VC
Eleocharis erythropoda	Red-stemmed spikerush	ELEERYT	Sedge	Native	VC
Eleocharis quadrangulata	Square-stemmed spikerush	ELEQUAD	Sedge	Native	VC
Eleocharis quinqueflora	Few-flowered spikerush	ELEPAUC	Sedge	Native	VC
Eleocharis sp.	Spikerush species	ELEOCH	Sedge	Native	VC
Elymus canadensis	Canada wildrye	ELYCANA	Grass	Native	VC
Elymus hystrix	Bottlebrush grass	HYSPATU	Grass	Native	VC
Elymus repens	Quackgrass	ELYREPE	Grass	Exotic	VC
Elymus riparius	Eastern riverbank wildrye	ELYRIPA	Grass	Native	VC
Elymus trachycaulus	Slender wildrye	ELYTRAC	Grass	Native	VC
Elymus villosus	Downy wildrye	ELYVILL	Grass	Native	VC
Elymus virginicus	Virginia wildrye	ELYVIRG	Grass	Native	VC
Epilobium ciliatum	Northern willowherb	EPICILI	Forb	Native	VC
Epilobium coloratum	Purple-veined willowherb	EPICOLO	Forb	Native	VC
Epilobium hirsutum	Hairy willowherb	EPIHIRS	Forb	Exotic	VC
Epilobium strictum	Downy willowherb	EPISTRI	Forb	Native	VC

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Epipactis helleborine	Broad-leaved helleborine	EPIHELL	Forb	Exotic	VC
Equisetum arvense	Field horsetail	EQUARVE	Fern	Native	VC
Equisetum hyemale	Common scouring-rush	EQUHYEM	Fern	Native	VC
Equisetum laevigatum	Smooth scouring-rush	EQULAEV	Fern	Native	VC
Equisetum pratense	Meadow horsetail	EQUPRAT	Fern	Native	VC
Equisetum variegatum	Variegated scouring-rush	EQUVARI	Fern	Native	VC
Erigeron annuus	Annual fleabane	ERIANNU	Forb	Native	VC
Erigeron canadensis	Canada horseweed	CONCANA	Forb	Native	VC
Erigeron philadelphicus	Philadelphia fleabane	ERIPHIL	Forb	Native	VC
Erigeron pulchellus	Robin's-plantain fleabane	ERIPULC	Forb	Native	VC
Euonymus atropurpureus	Eastern burning-bush	EUOATRO	Shrub	Native	VC
Euonymus europaeus	European euonymus	EUOEURO	Shrub	Exotic	B
Eupatorium altissimum	Tall boneset	EUPALTI	Forb	Native	VC
Eupatorium perfoliatum	Common boneset	EUPPERF	Forb	Native	VC
Euphorbia polygonifolia	Seaside spurge	CHAPOLY	Forb	Native	VC
Euphorbia virgata	Leafy spurge	EUPESUL	Forb	Exotic	VC
Euthamia graminifolia	Grass-leaved goldenrod	EUTGRAM	Forb	Native	VC
Fallopia convolvulus	Eurasian black bindweed	POLCONV	Vine	Exotic	VC
Festuca rubra	Red fescue	FESRUBR	Grass	Exotic	VC
Festuca sp.	Fescue species	FESTUC	Grass	n/a	VC
Festuca subverticillata	Nodding fescue	FESSUBV	Grass	Native	VC
Fragaria vesca	American woodland strawberry	FRAVESC	Forb	Native	VC
Fragaria virginiana	Wild strawberry	FRAVIRG	Forb	Native	VC
Fraxinus americana	White ash	FRAAMER	Tree	Native	VC
Fraxinus pennsylvanica	Red ash	FRAPENN	Tree	Native	B
Fraxinus sp.	Ash species	FRAXIN	Tree	Native	B
Galium aparine	Common bedstraw	GALAPAR	Forb	Native	VC
Galium asprellum	Rough bedstraw	GALASPR	Forb	Native	VC
Galium circaezans	Licorice bedstraw	GALCIRC	Forb	Native	VC
Galium lanceolatum	Lance-leaved wild licorice	GALLANC	Forb	Native	VC
Galium mollugo	Smooth bedstraw	GALMOLL	Forb	Exotic	VC
Galium palustre	Common marsh bedstraw	GALPALU	Forb	Native	VC
Galium pilosum	Hairy bedstraw	GALPILO	Forb	Native	VC

(Continues)

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Galium tinctorium	Dyer's bedstraw	GALTINC	Forb	Native	VC
Galium triflorum	Three-flowered bedstraw	GALTRIF	Forb	Native	VC
Gentiana andrewsii	Andrews' bottle gentian	GENANDR	Forb	Native	VC
Geranium robertianum	Herb-robert	GERROBE	Forb	Native	VC
Geum canadense	Canada avens	GEUCANA	Forb	Native	VC
Glyceria striata	Fowl mannagrass	GLYSTRI	Grass	Native	VC
Gnaphalium uliginosum	Low cudweed	GNAULIG	Forb	Exotic	VC
Helenium autumnale	Common sneezeweed	HELAUTU	Forb	Native	VC
Hesperostipa spartea	Plains porcupine grass	STISPAR	Grass	Native	VC
Hieracium sp.	n/a	HIERAC	Forb	n/a	VC
Hydrocharis morsus-ranae	European frog-bit	HYDMORS	Forb	Exotic	VC
Hypericum canadense	Canada St. John's-wort	HYPCANA	Forb	Native	VC
Hypericum kalmianum	Kalm's St. John's-wort	HYPKALM	Shrub	Native	B
Hypericum majus	Large St. John's-wort	HYPMAJU	Forb	Native	VC
Hypericum perforatum	Common St. John's-wort	HYPPERF	Forb	Exotic	VC
Hypericum punctatum	Spotted St. John's-wort	HYPPUNC	Forb	Native	VC
Ilex verticillata	Common winterberry	ILEVERT	Shrub	Native	B
Impatiens capensis	Spotted jewelweed	IMPCAPE	Forb	Native	VC
Impatiens pallida	Pale jewelweed	IMPPALL	Forb	Native	VC
Iris sp.	n/a	IRIS…	Forb	n/a	VC
Iris versicolor	Harlequin blue flag	IRIVERS	Forb	Native	VC
Iris virginica	Southern blue flag	IRIVIRG	Forb	Native	VC
Juncus balticus	Baltic rush	JUNBALT	Forb	Native	VC
Juncus dudleyi	Dudley's rush	JUNDUDL	Forb	Native	VC
Juncus effusus	Soft rush	JUNEFFU	Forb	Native	VC
Juncus nodosus	Knotted rush	JUNNODO	Forb	Native	VC
Juncus tenuis	Path rush	JUNTEAN	Forb	Native	VC
Juniperus communis var. *depressa*	Depressed juniper	JUNCOMM	Shrub	Native	B
Juniperus virginiana	Eastern red cedar	JUNVIRG	Tree	Native	B
Kali tragus	Prickly russian thistle	SALKALI	Forb	Exotic	VC
Lactuca biennis	Tall blue lettuce	LACBIEN	Forb	Native	VC
Lactuca canadensis	Canada lettuce	LACCANA	Forb	Native	VC
Lactuca sp.	n/a	LACTUC	Forb	n/a	VC

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Larix laricina	Tamarack	LARLARI	Tree	Native	B
Lathyrus japonicus	Beach pea	LATJAPO	Forb	Native	VC
Lathyrus palustris	Marsh vetchling	LATPALU	Forb	Native	VC
Leersia oryzoides	Rice cutgrass	LEEORYZ	Grass	Native	VC
Leersia virginica	White cutgrass	LEEVIRG	Grass	Native	VC
Lemna minor	Small duckweed	LEMMINO	Forb	Native	VC
Lemna trisulca	Star duckweed	LEMTRIS	Forb	Native	VC
Leonurus cardiaca	Common motherwort	LEOCARD	Forb	Exotic	VC
Liatris cylindracea	Slender blazing-star	LIACYLI	Forb	Native	VC
Lichen sp.	Lichen species	LICHEN	Lichen	Native	VC
Linaria vulgaris	Butter-and-eggs	LINVULG	Forb	Exotic	VC
Linnaea borealis	Twinflower	LINBORE	Forb	Native	VC
Linum medium	Stiff yellow flax	LINMEDI	Forb	Native	VC
Liparis loeselii	Loesel's twayblade	LIPLOES	Forb	Native	VC
Liriodendron tulipifera	Tulip tree	LIRTULI	Tree	Native	WC
Lithospermum canescens	Hoary puccoon	LITCANE	Forb	Native	VC
Lithospermum caroliniense	Golden puccoon	LITCARO	Forb	Native	VC
Lithospermum officinale	European gromwell	LITOFFI	Forb	Exotic	VC
Lolium perenne	Perennial ryegrass	LOLPERE	Grass	Exotic	VC
Lonicera hirsuta	Hairy honeysuckle	LONHIRS	Vine	Native	WC
Ludwigia palustris	Marsh seedbox	LUDPALU	Forb	Native	VC
Lycopus americanus	American water-horehound	LYCAMER	Forb	Native	VC
Lycopus uniflorus	Northern water-horehound	LYCUNIF	Forb	Native	VC
Lysimachia borealis	Northern starflower	TRIBORE	Forb	Native	VC
Lysimachia terrestris	Swamp yellow loosestrife	LYSTERR	Forb	Native	VC
Lysimachia thyrsiflora	Tufted yellow loosestrife	LYSTHYR	Forb	Native	VC
Lythrum salicaria	Purple loosestrife	LYTSALI	Forb	Exotic	VC
Maianthemum canadense	Wild lily-of-the-valley	MAICANA	Forb	Native	VC
Maianthemum racemosum	Large false Solomon's seal	MAIRACE	Forb	Native	VC
Maianthemum stellatum	Star-flowered false Solomon's seal	MAISTEL	Forb	Native	VC
Melampyrum lineare	American cow-wheat	MELLINE	Forb	Native	VC

(Continues)

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Melilotus albus	White sweet-clover	MELALBA	Forb	Exotic	VC
Mentha sp.	Mint species	MENTHA	Forb	n/a	VC
Moehringia lateriflora	Grove sandwort	MOELATE	Forb	Native	VC
Monarda fistulosa	Wild bergamot	MONFIST	Forb	Native	VC
Moss sp.	Moss species	MOSS	Bryophyte	Native	VC
Muhlenbergia frondosa	Leafy muhly	MUHFRON	Grass	Native	VC
Muhlenbergia mexicana	Mexican muhly	MUHMEXI	Grass	Native	VC
Muhlenbergia tenuiflora	Slim-flowered muhly	MUHTENU	Grass	Native	VC
Myriophyllum heterophyllum	Variable-leaved water-milfoil	MYRHETE	Forb	Native	VC
Najas flexilis	Slender naiad	NAJFLEX	Forb	Native	VC
Nasturtium officinale	Watercress	NASOFFI	Forb	Exotic	VC
Nepeta cataria	Catnip	NEPCATA	Forb	Exotic	VC
Nuphar variegata	Variegated pond-lily	NUPVARI	Forb	Native	VC
Oenothera biennis	Common evening-primrose	OENBIEN	Forb	Native	VC
Oenothera perennis	Perennial evening-primrose	OENPERE	Forb	Native	VC
Onoclea sensibilis	Sensitive fern	ONOSENS	Fern	Native	VC
Ophioglossum pusillum	Northern adder's-tongue	OPHPUSI	Fern	Native	VC
Origanum vulgare	Wild marjoram	ORIVULG	Forb	Exotic	VC
Oryzopsis asperifolia	Rough-leaved mountain rice	ORYASPE	Grass	Native	VC
Ostrya virginiana	Eastern hop-hornbeam	OSTVIRG	Tree	Native	B
Packera aurea	Golden groundsel	SENAURE	Forb	Native	VC
Palustricodon aparinoides	Marsh bellflower	CAMAPAR	Forb	Native	VC
Panicum virgatum	Old switch panicgrass	PANVIRG	Grass	Native	VC
Parietaria pensylvanica	Pennsylvania pellitory	PARPENS	Forb	Native	VC
Parnassia glauca	Fen grass-of-parnassus	PARGLAU	Forb	Native	VC
Parthenocissus vitacea	Thicket creeper	PARINSE	Vine	Native	B
Patis racemosa	Black-seed ricegrass	ORYRACE	Grass	Native	VC
Persicaria amphibia	Water smartweed	POLAMPH	Forb	Native	VC
Persicaria hydropiper	Marshpepper smartweed	POLHYDR	Forb	Exotic	VC
Persicaria maculosa	Spotted lady's-thumb	POLPERS	Forb	Exotic	VC
Persicaria sagittata	Arrow-leaved smartweed	POLSAGI	Forb	Native	VC

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Phalaris arundinacea	Reed canarygrass	PHAARUN	Grass	Exotic	VC
Phragmites australis ssp. *australis*	European reed	PHRAUST	Grass	Exotic	VC
Physalis heterophylla	Clammy ground-cherry	PHYHETE	Forb	Native	VC
Pilea fontana	Lesser clearweed	PILFONT	Forb	Native	VC
Pilosella caespitosa	Meadow hawkweed	HIECAES	Forb	Exotic	VC
Pinus strobus	Eastern white pine	PINSTRO	Tree	Native	B
Plantago major	Common plantain	PLAMAJO	Forb	Exotic	VC
Platanthera hyperborea	Leafy northern green orchid	PLAHYPE	Forb	Native	VC
Poa compressa	Canada bluegrass	POACOMP	Grass	Exotic	VC
Poa pratensis	Kentucky bluegrass	POAPRAT	Grass	Exotic	VC
Polanisia dodecandra	Common clammyweed	POLDODE	Forb	Native	VC
Polygala polygama	Racemed milkwort	POLPOLY	Forb	Native	VC
Polygonatum pubescens	Hairy Solomon's seal	POLPUBE	Forb	Native	VC
Polygonatum sp.	n/a	POLYGO	Forb	Native	VC
Populus deltoides	Eastern cottonwood	POPDELT	Tree	Native	B
Potamogeton amplifolius	Large-leaved pondweed	POTAMPL	Forb	Native	VC
Potamogeton gramineus	Grass-leaved pondweed	POTGRAM	Forb	Native	VC
Potamogeton illinoensis	Illinois pondweed	POTILLI	Forb	Native	VC
Potamogeton natans	Floating-leaved pondweed	POTNATA	Forb	Native	VC
Potamogeton sp.	n/a	POTAMO	Forb	Native	VC
Potentilla anserina	Silverweed	POTANSE	Forb	Native	VC
Prenanthes sp.	n/a	PRENAN	Forb	Native	VC
Proserpinaca palustris	Marsh mermaidweed	PROPALU	Forb	Native	VC
Prunella vulgaris	Lance-leaved self-heal	PRUVULG	Forb	Native	VC
Prunus serotina	Black cherry	PRUSERO	Tree	Native	B
Prunus sp.	Cherry species	PRUNUS	Unknown	Native	B
Prunus virginiana	Chokecherry	PRUVIRG	Shrub	Native	B
Pseudognaphalium obtusifolium	Fragrant cudweed	GNAOBTU	Forb	Native	VC
Pteridium aquilinum	Bracken fern	PTEAQUI	Fern	Native	VC
Quercus alba	White oak	QUEALBA	Tree	Native	VC
Quercus muehlenbergii	Chinquapin oak	QUEMUEH	Tree	Native	B

(Continues)

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Quercus rubra	Northern red oak	QUERUBR	Tree	Native	B
Quercus velutina	Black oak	QUEVELU	Tree	Native	B
Ranunculus abortivus	Kidney-leaved buttercup	RANABOR	Forb	Native	VC
Rhamnus cathartica	European buckthorn	RHACATH	Tree	Exotic	WC
Rhus typhina	Staghorn sumac	RHUTYPH	Shrub	Native	B
Rhynchospora capillacea	Slender beakrush	RHYCAPI	Sedge	Native	VC
Riccia sp.	n/a	RICCIA	Bryophyte	Native	VC
Rosa blanda	Smooth rose	ROSBLAN	Shrub	Native	WC
Rosa multiflora	Multiflora rose	ROSMULT	Shrub	Exotic	B
Rosa palustris	Swamp rose	ROSPALU	Shrub	Native	B
Rosa rubiginosa	Sweetbriar rose	ROSRUBI	Shrub	Exotic	B
Rosa sp.	Rose species	ROSA…	Shrub	n/a	VC
Rubus allegheniensis	Allegheny blackberry	RUBALLE	Shrub	Native	B
Rubus idaeus ssp. strigosus	North American red raspberry	RUBIDAE	Shrub	Native	B
Rubus occidentalis	Black raspberry	RUBOCCI	Shrub	Native	B
Rumex acetosella	Sheep sorrel	RUMACET	Forb	Exotic	VC
Rumex crispus	Curled dock	RUMCRIS	Forb	Exotic	VC
Rumex obtusifolius	Bitter dock	RUMOBTU	Forb	Exotic	VC
Rumex sp.	n/a	RUMEX	Forb	n/a	VC
Rumex verticillatus	Swamp dock	RUMVERT	Forb	Native	VC
Sagittaria latifolia	Broad-leaved arrowhead	SAGLATI	Forb	Native	VC
Salix interior	Sandbar willow	SALEXIG	Shrub	Native	WC
Sambucus canadensis	Common elderberry	SAMCANA	Shrub	Native	B
Sambucus racemosa	Red elderberry	SAMPUBE	Shrub	Native	WC
Sassafras albidum	Sassafras	SASALBI	Tree	Native	B
Schizachne purpurascens	Purple false melic	SCHPURP	Grass	Native	VC
Schizachyrium scoparium	Little bluestem	SCHSCOP	Grass	Native	VC
Schoenoplectus acutus	Hard-stemmed bulush	SCIACUT	Sedge	Native	VC
Schoenoplectus pungens	Common three-square bulrush	SCIPUNG	Sedge	Native	VC
Schoenoplectus tabernaemontani	Soft-stemmed bulrush	SCIVALI	Sedge	Native	VC
Scleria verticillata	Low nutrush	SCLVERT	Sedge	Native	VC
Scutellaria galericulata	Marsh skullcap	SCUGALE	Forb	Native	VC

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Scutellaria lateriflora	Mad-dog skullcap	SCULATE	Forb	Native	VC
Seedling sp.	Unknown seedling species	SEEDLNG	Unknown	n/a	VC
Selaginella eclipes	Hidden spikemoss	SELAPOD	Fern	Native	VC
Silene antirrhina	Sleepy catchfly	SILANTI	Forb	Native	VC
Sisyrinchium montanum	Strict blue-eyed-grass	SISMONT	Forb	Native	VC
Solanum dulcamara	Bittersweet nightshade	SOLDULC	Vine	Exotic	VC
Solidago altissima	Tall goldenrod	SOLALTI	Forb	Native	VC
Solidago caesia	Blue-stemmed goldenrod	SOLCAES	Forb	Native	VC
Solidago canadensis	Canada goldenrod	SOLCANA	Forb	Native	VC
Solidago canadensis complex	Canada goldenrod	SOLCASL	Forb	Native	VC
Solidago gigantea	Giant goldenrod	SOLGIGA	Forb	Native	VC
Solidago hispida	Hairy goldenrod	SOLHISP	Forb	Native	VC
Solidago nemoralis	Grey-stemmed goldenrod	SOLNEMO	Forb	Native	VC
Solidago ohioensis	Ohio goldenrod	SOLOHIO	Forb	Native	VC
Solidago ptarmicoides	Upland white goldenrod	SOLPTAR	Forb	Native	VC
Sonchus arvensis	Field sow-thistle	SONARVE	Forb	Exotic	VC
Sonchus sp.	n/a	SONCHU	Forb	Exotic	VC
Sorghastrum nutans	Yellow indiangrass	SORNUTA	Grass	Native	VC
Sparganium eurycarpum	Broad-fruited burreed	SPAEURY	Forb	Native	VC
Spiraea alba	White meadowsweet	SPIALBA	Shrub	Native	WC
Spirodela polyrhiza	Great duckweed	SPIPOLY	Forb	Native	VC
Sporobolus cryptandrus	Sand dropseed	SPOCRYP	Grass	Native	VC
Sporobolus michauxianus	Prairie cordgrass	SPAPECT	Grass	Native	VC
Stachys hispida	Hispid hedge-nettle	STAHISP	Forb	Native	VC
Stachys palustris	Marsh hedge-nettle	STAPALU	Forb	Exotic	VC
Stachys sp.	n/a	STACHY	Forb	n/a	VC
Stellaria graminea	Grass-leaved starwort	STEGRAM	Forb	Exotic	VC
Stellaria longifolia	Long-leaved starwort	STELONG	Forb	Native	VC
Stellaria media	Common chickweed	STEMEDI	Forb	Exotic	VC
Stellaria pallida	Pale starwort	STEPALL	Forb	Exotic	VC
Symphoricarpos albus var. *albus*	Thin-leaved snowberry	SYMALBU	Shrub	Native	B
Symphyotrichum boreale	Rush aster	ASTBORE	Forb	Native	VC
Symphyotrichum dumosum	Bushy aster	ASTDUMO	Forb	Native	VC

(Continues)

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Symphyotrichum ericoides	White heath aster	ASTERIC	Forb	Native	VC
Symphyotrichum lanceolatum	Panicled aster	ASTLANC	Forb	Native	VC
Symphyotrichum lateriflorum	Calico aster	ASTLATE	Forb	Native	VC
Symphyotrichum oolentangiense	Sky blue aster	ASTOOLE	Forb	Native	VC
Symphyotrichum sp.	n/a	ASTER	Forb	Native	VC
Symphyotrichum urophyllum	Arrow-leaved aster	ASTUROP	Forb	Native	VC
Taraxacum officinale	Common dandelion	TAROFFI	Forb	Exotic	VC
Teucrium canadense	Canada germander	TEUCANA	Forb	Native	VC
Thalictrum sp.	n/a	THALIC	Forb	n/a	VC
Thelypteris palustris	Marsh fern	THEPALU	Fern	Native	VC
Thlaspi arvense	Field pennycress	THLARVE	Forb	Exotic	VC
Thuja occidentalis	Eastern white cedar	THUOCCI	Tree	Native	B
Tilia americana	Basswood	TILAMER	Tree	Native	B
Toxicodendron radicans	Poison ivy	RHURADI	Shrub	Native	B
Tragopogon dubius	Yellow goatsbeard	TRADUBI	Forb	Exotic	VC
Tragopogon pratensis	Meadow goatsbeard	TRAPRAT	Forb	Exotic	VC
Tragopogon sp.	n/a	TRAGOP	Forb	Exotic	VC
Triadenum fraseri	Fraser's St. John's-wort	TRIFRAS	Forb	Native	VC
Triglochin maritima	Seaside arrowgrass	TRIMARI	Forb	Native	VC
Triglochin sp.	Arrowgrass species	TRIGLO	Forb	Native	VC
Trillium grandiflorum	White trillium	TRIGRAN	Forb	Native	VC
Turritis glabra	Tower mustard	ARAGLAB	Forb	Native	VC
Typha angustifolia	Narrow-leaved cattail	TYPANGU	Forb	Exotic	VC
Typha latifolia	Broad-leaved cattail	TYPLATI	Forb	Native	VC
Typha x glauca	(Typha angustifolia × Typha latifolia)	TYPXGLA	Forb	Exotic	VC
Unknown Poaceae	Unknown grass species	GRASS	Grass	n/a	VC
Unknown sp.	Unknown species	UNKNOWN	Unknown	n/a	B
Urtica dioica ssp. *dioica*	European stinging nettle	URTDIDI	Forb	Exotic	VC
Utricularia cornuta	Horned bladderwort	UTRCORN	Forb	Native	VC
Utricularia gibba	Humped bladderwort	UTRGIBB	Forb	Native	VC
Utricularia intermedia	Flat-leaved bladderwort	UTRINTE	Forb	Native	VC
Utricularia resupinata	Northeastern bladderwort	UTRRESU	Forb	Native	VC

TABLE A2 (Continued)

Scientific name	Common name	Species code	Growth form[a]	Occurrence status[b]	Dataset[c]
Utricularia subulata	Zigzag bladderwort	UTRSUBU	Forb	n/a	VC
Utricularia vulgaris	Common bladderwort	UTRVULG	Forb	Native	VC
Verbascum thapsus	Common mullein	VERTHAP	Forb	Exotic	VC
Verbena hastata	Blue vervain	VERHAST	Forb	Native	VC
Verbena urticifolia	White vervain	VERURTI	Forb	Native	VC
Veronica arvensis	Corn speedwell	VERARVE	Forb	Exotic	VC
Veronica officinalis	Common speedwell	VEROFFI	Forb	Exotic	VC
Veronica peregrina	Purslane speedwell	VERPERE	Forb	Native	VC
Veronica persica	Bird's-eye speedwell	VERPERS	Forb	Exotic	VC
Veronica scutellata	Marsh speedwell	VERSCUT	Forb	Native	VC
Veronica serpyllifolia	Thyme-leaved speedwell	VERSERP	Forb	Exotic	VC
Viburnum lentago	Nannyberry	VIBLENT	Shrub	Native	WC
Viola cucullata	Marsh blue violet	VIOCUCU	Forb	Native	VC
Viola rostrata	Long-spurred violet	VIOROST	Forb	Native	VC
Viola sp.	Violet species	VIOLA	Forb	Native	VC
Vitis aestivalis	Summer grape	VITAEST	Vine	Native	B
Vitis riparia	Riverbank grape	VITRIPA	Vine	Native	VC
Wolffia columbiana	Columbia watermeal	WOLCOLU	Forb	Native	VC

[a]Growth form refers to the defined vegetation species form of forb, grass, sedge, tree, shrub, fern, bryophyte, vine, and unknown, adapted from Bradstreet et al. (1992).

[b]Occurrence status refers to whether a species is considered native, exotic, or of unknown distribution in Ontario, adapted from the Natural Heritage Information Centre (2021).

[c]Dataset identifies whether the species is recorded from the woody count dataset (WC), vegetation cover dataset (VC), or from both the woody count and vegetation cover datasets (B).

TABLE A3 Summary table of vegetation species recorded during vegetation monitoring from 1992–2021 at Long Point, Ontario, Canada that are browse-sensitive, with supporting references from multiple studies.

Species	References
Wild lily-of-the-valley	Bradshaw and Waller (2016), Frerker et al. (2014), Goetsch et al. (2011), Kirschbaum and Anacker (2005), Rooney (1997, 2001), Royo et al. (2010).
Eastern white pine	Anderson and Loucks (1979), Bradshaw and Waller (2016), Rooney and Waller (2003).
Northern red oak	Anderson and Loucks (1979), Blossey et al. (2019), Bradshaw and Waller (2016), Rooney and Waller (2003).
Allegheny blackberry	Goetsch et al. (2011), Horsley et al. (2003), Royo et al. (2010), Trumbull et al. (1989).
Eastern white cedar	Anderson and Loucks (1979), Bradshaw and Waller (2016), Cornett et al. (2000), Rooney (2001), Rooney and Waller (2003), Waller and Alverson (1997), White (2012).
White trillium	Augustine and Frelich (1998), Bradshaw and Waller (2016), Frerker et al. (2014), Royo et al. (2010).

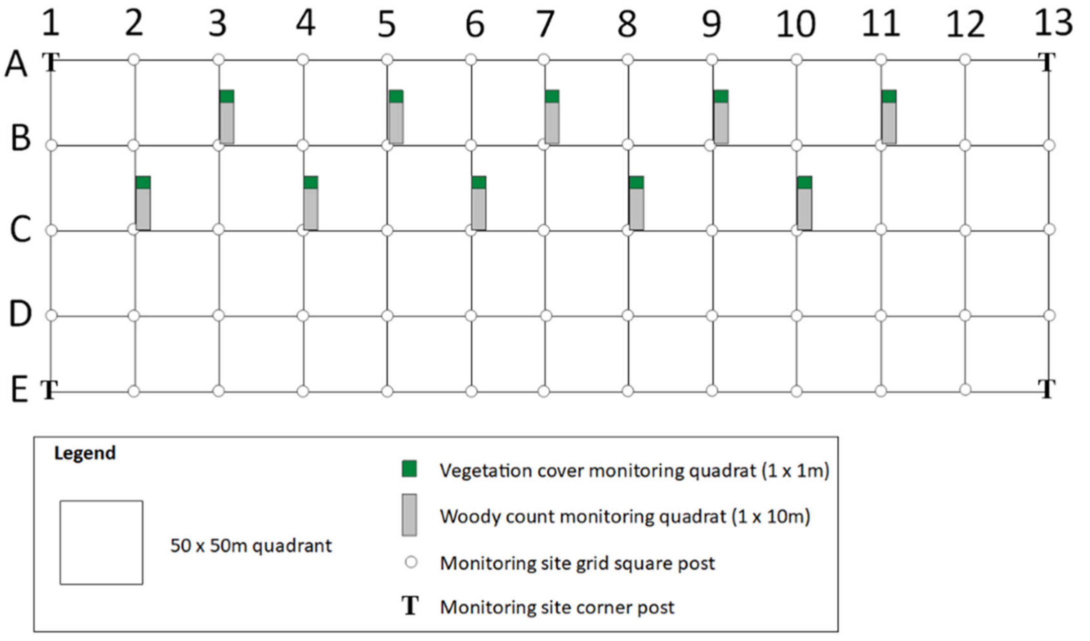

FIGURE A1 Schematic example of a monitoring site grid layout, and the associated sampling quadrats for the woody count and vegetation cover datasets, collected between 1992–2021 from the Long Point Breeding Bird Census monitoring project at Long Point, Ontario, Canada.

APPENDIX B: GENERALIZED LINEAR MIXED MODEL RESULTS

TABLE B1 Summary of generalized linear mixed model results to explain variation in species richness from the woody count dataset (n = 3,439, df = 3,438) collected at Long Point, Ontario, Canada, with year (1992–2021) as a fixed effect, and monitoring site and quadrat as random effects.

Term	β ± SE	Z	P	Variance	SD
Random effects					
Quadrat				0.19	0.44
Monitoring site				0.10	0.32
Fixed effects					
Intercept	0.50 ± 0.12	4.39	<0.001		
Year	0.63 ± 0.08	7.73	<0.001		

TABLE B2 Summary of generalized linear mixed model results to explain variation in species richness from the vegetation cover dataset (n = 3,375, df = 3,374) collected at Long Point, Ontario, Canada, with year (1992–2021) as a fixed effect, and monitoring site and quadrat as random effects.

Term	β ± SE	Z	P	Variance	SD
Random effects					
Quadrat				0.14	0.37
Monitoring site				0.06	0.24
Fixed effects					
Intercept	1.80 ± 0.08	24.05	<0.001		
Year	0.09 ± 0.04	1.97	0.05		

TABLE B3 Summary of generalized linear mixed model results to explain variation in woody stem abundance within the browse layer (0–2.0 m) from the woody count dataset (n = 3,439, df = 3,438) collected at Long Point, Ontario, Canada, with year (1992–2021) as a fixed effect, and monitoring site and quadrat as random effects.

Term	β ± SE	Z	P	Variance	SD
Random effects					
Quadrat				1.19	1.09
Monitoring site				0.36	0.60
Fixed effects					
Intercept	3.43 ± 0.18	18.81	<0.001		
Year	−0.01 ± 0.02	−0.52	0.60		

TABLE B4 Summary of generalized linear mixed model results to explain variation in woody stem abundance above the browse layer (≥2.0 m) from the woody count dataset (n = 297, df = 296) collected at Long Point, Ontario, Canada, with year (1992–1994) as a fixed effect, and monitoring site and quadrat as random effects.

Term	β ± SE	Z	P	Variance	SD
Random effects					
Quadrat				3.30	1.82
Monitoring site				2.43	1.56
Fixed effects					
Intercept	−4.03 ± 0.52	−7.71	<0.001		
Year	−0.10 ± 0.40	−0.24	>0.81		

TABLE B5 Summary of generalized linear mixed model results to explain variation in woody stem abundance above the browse layer (≥2.0 m) from the woody count dataset (*n* = 3,142, df = 3,141) collected at Long Point, Ontario, Canada, with year (1995–2021) as a fixed effect, and monitoring site and quadrat as random effects.

Term	β ± SE	*Z*	*P*	Variance	SD
Random effects					
Quadrat				3.29	1.81
Monitoring site				2.44	1.56
Fixed effects					
Intercept	−3.11 ± 0.48	−6.53	<0.001		
Year	1.83 ± 0.19	9.84	<0.001		

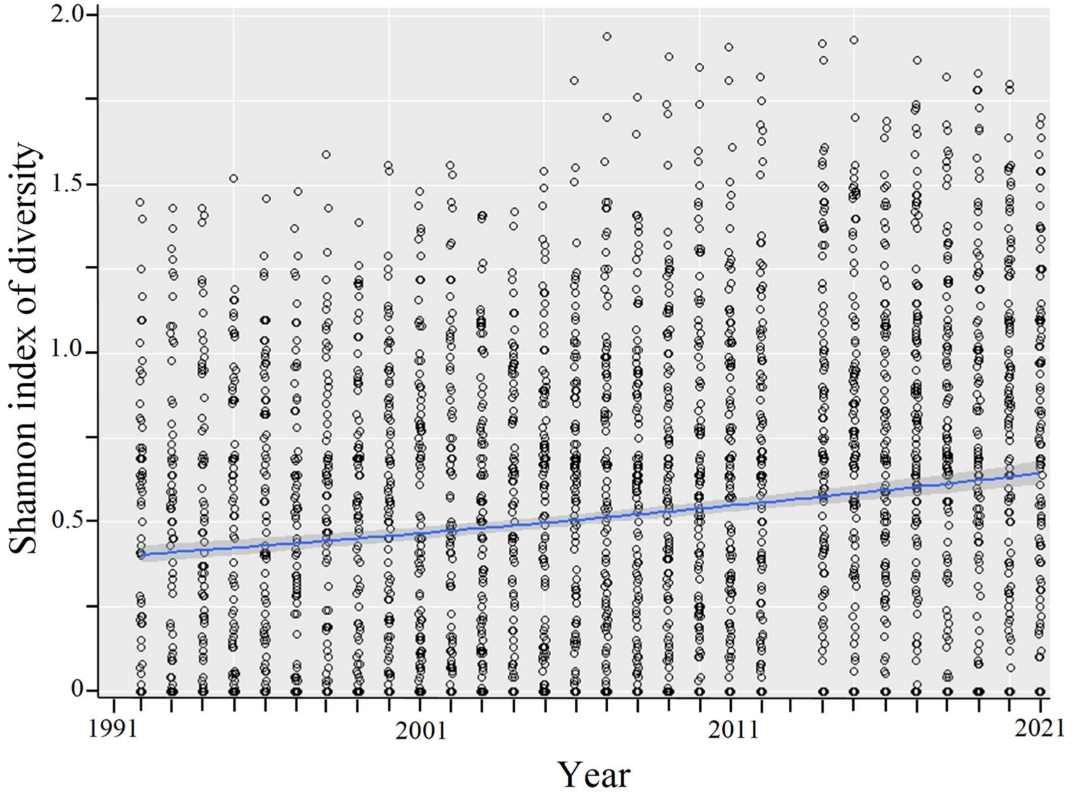

FIGURE B1 Results of the 2-part hurdle model showing the mean estimate (blue line), and 95% confidence interval (shaded grey) of species diversity (Shannon index of diversity) of woody stem counts from 1992–2021 at Long Point, Ontario, Canada. Circles represent species diversity estimates at each sampling quadrat during each sampling year.

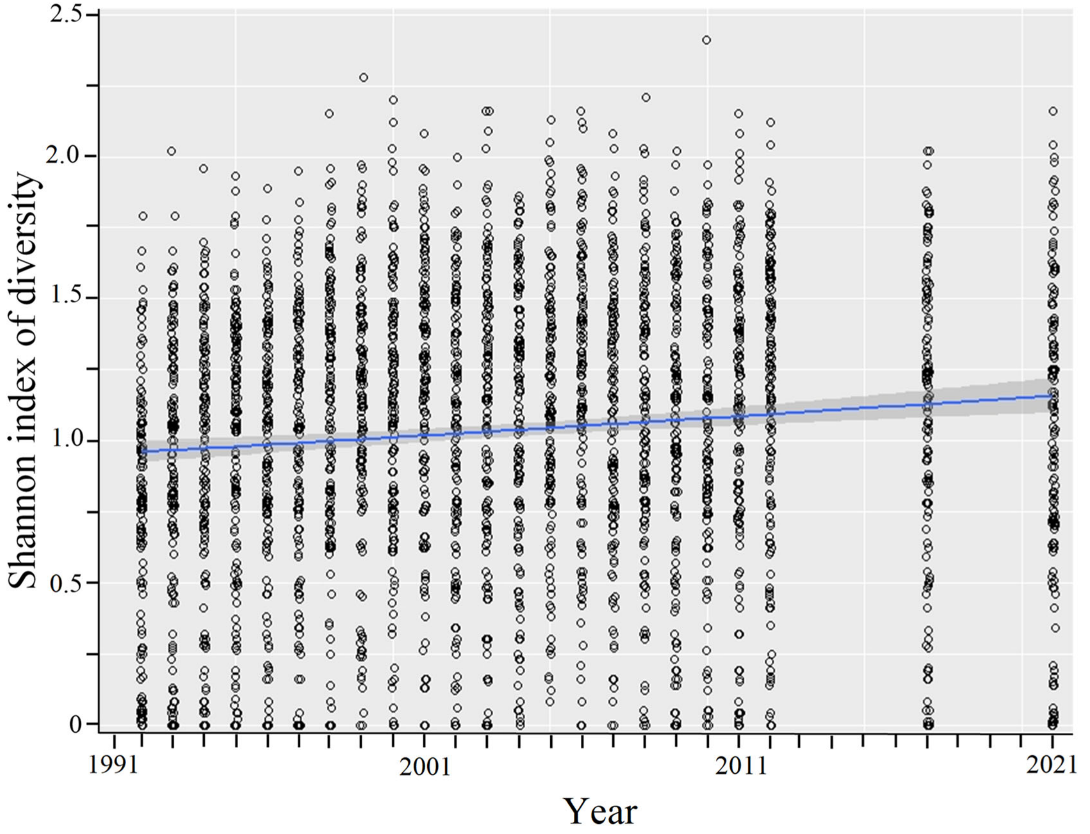

FIGURE B2 Results of the 2-part hurdle model showing the mean estimate (blue line), and 95% confidence interval (shaded grey) of species diversity (Shannon index of diversity) of vegetation cover estimates from 1992–2021 at Long Point, Ontario, Canada. Circles represent species diversity estimates at each sampling quadrat during each sampling year.

APPENDIX C: ZERO-ONE-INFLATED BETA DISTRIBUTION MODEL RESULTS

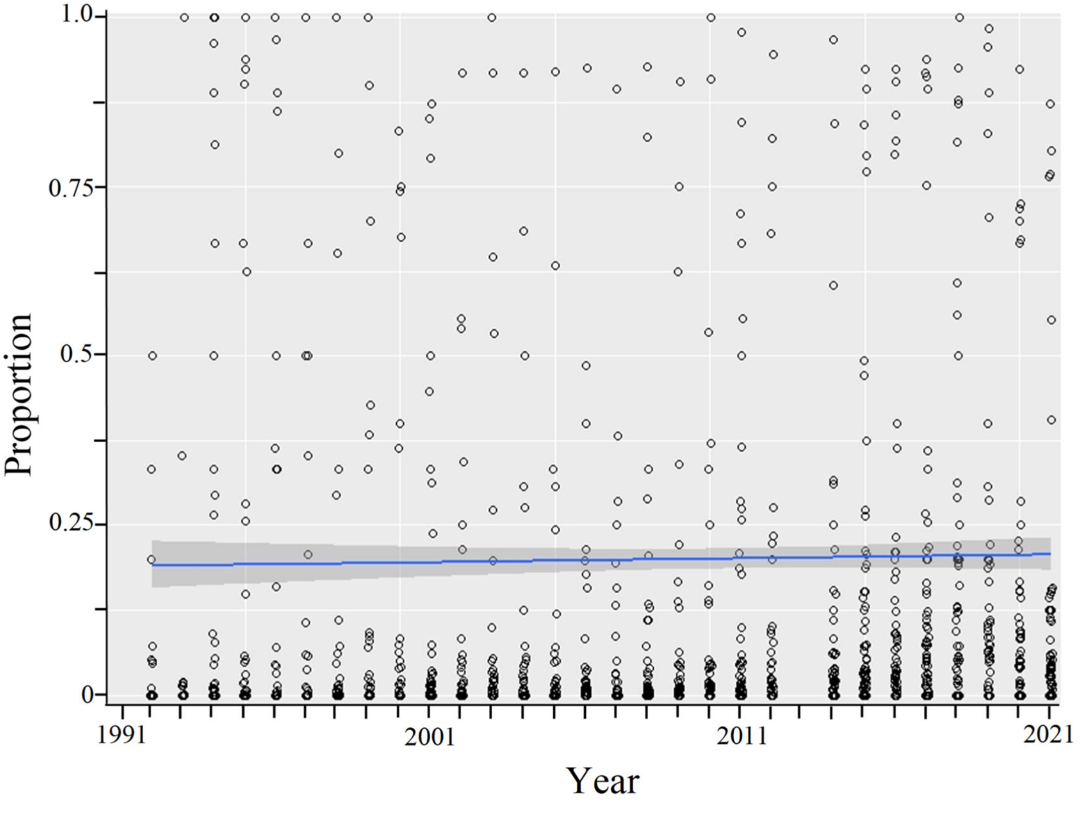

FIGURE C1 Results of the zero-one-inflated beta distribution model showing the mean estimate (blue line), and 95% confidence interval (shaded grey) of the proportional abundance of browse-sensitive woody stems (compared to non-browse-sensitive woody stems) from 1992–2021 at Long Point, Ontario, Canada. Circles represent the proportional abundance of browse-sensitive woody stems at each sampling quadrat during each sampling year.

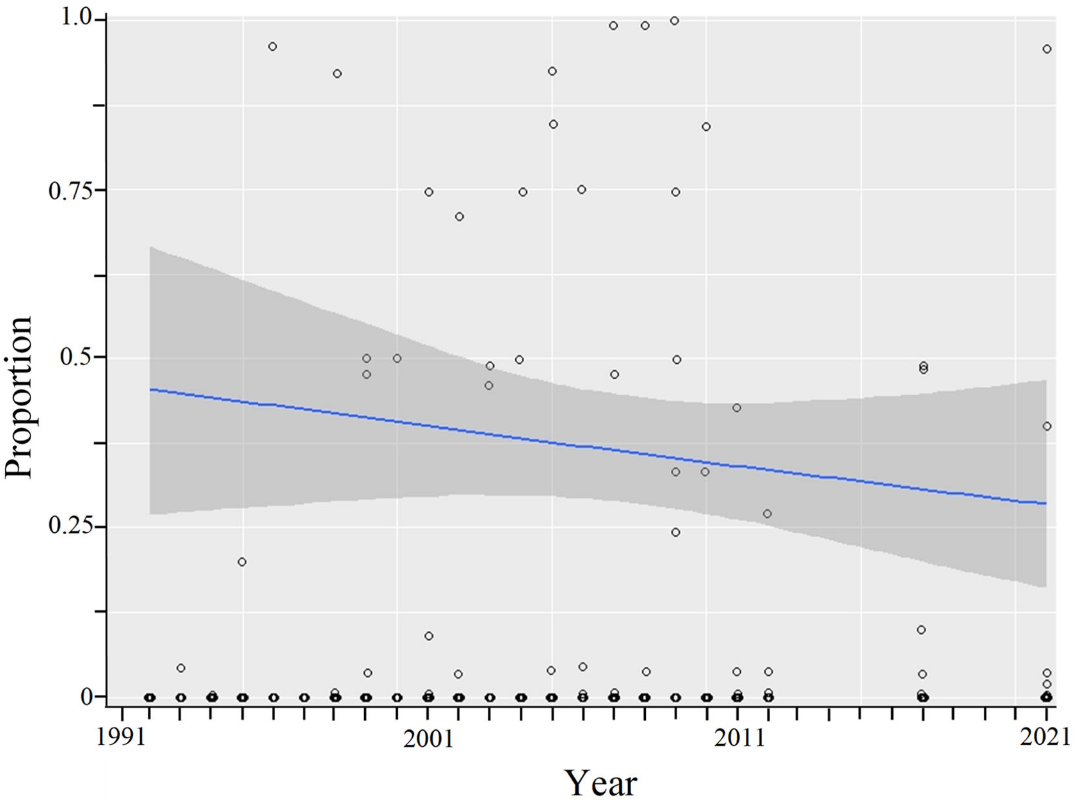

FIGURE C2 Results of the zero-one-inflated beta distribution model showing the mean estimate (blue line), and 95% confidence interval (shaded grey) of the proportional abundance of browse-sensitive forbs (compared to non-browse-sensitive forbs) from 1992–2021 at Long Point, Ontario, Canada. Circles represent the proportional abundance of browse-sensitive forbs at each sampling quadrat during each sampling year.

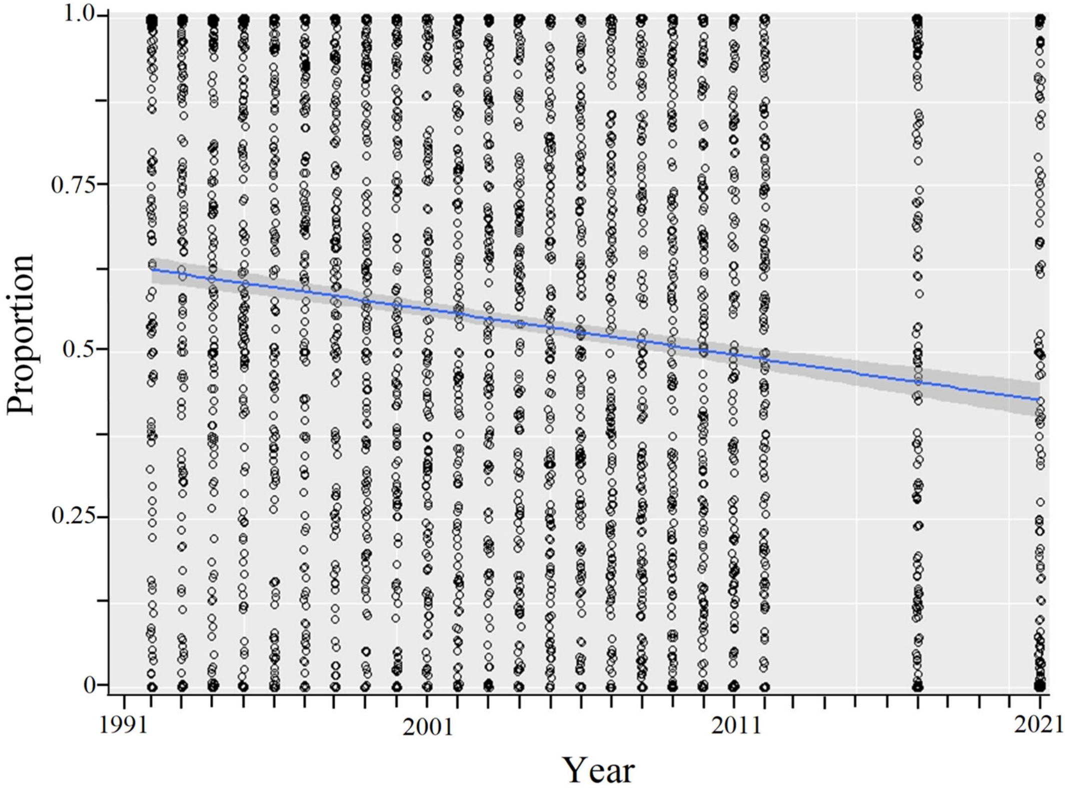

FIGURE C3 Results of the zero-one-inflated beta distribution model showing the mean estimate (blue line), and 95% confidence interval (shaded grey) of the proportional abundance of non-preferred species (i.e., grasses, ferns, and sedges) as compared to preferred species (i.e., bryophytes, forbs, lichen, shrubs, trees, and vines) from 1992–2021 at Long Point, Ontario, Canada. Circles represent the proportional abundance of non-preferred species (i.e., grasses, ferns, and sedges) at each sampling quadrat during each sampling year.

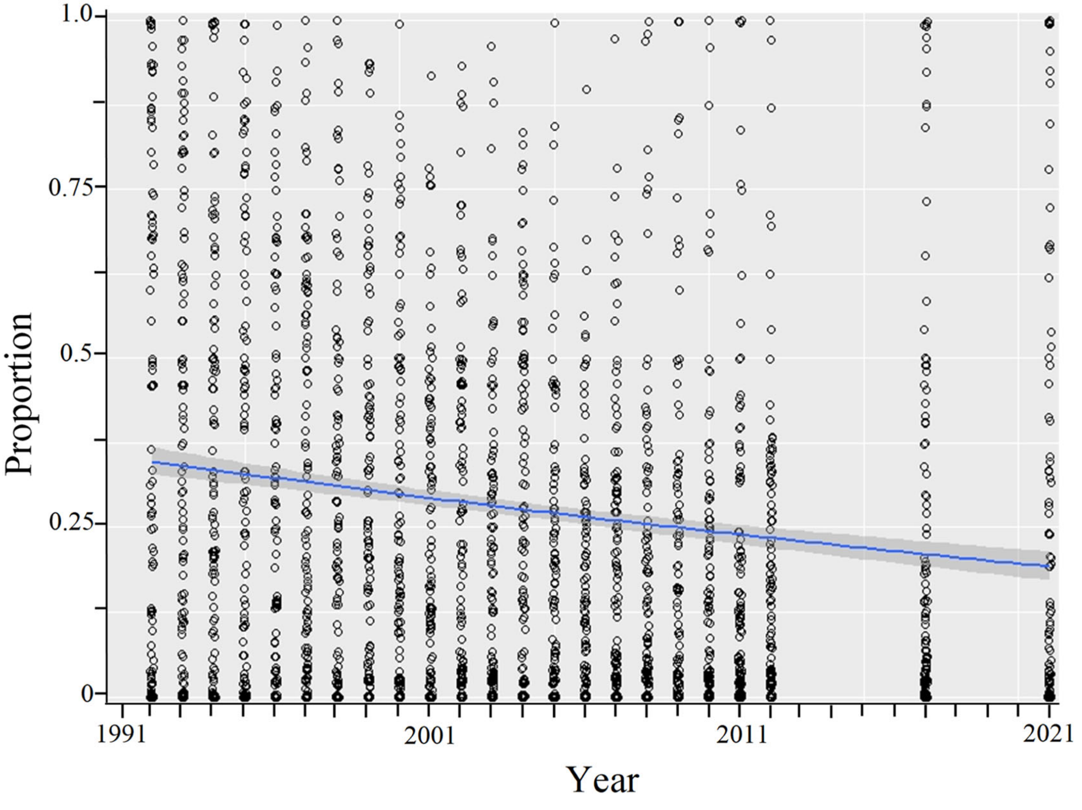

FIGURE C4 Results of the zero-one-inflated beta distribution model showing the mean estimate (blue line), and 95% confidence interval (shaded grey) of the proportional abundance of exotic species as compared to native species from 1992–2021 at Long Point, Ontario, Canada. Circles represent the proportional abundance of exotic species at each sampling quadrat during each sampling year.

APPENDIX D: NEW NATIVE AND EXOTIC SPECIES

TABLE D1 List of all new vegetation species sampled from the vegetation cover dataset from 1993–2021 at Long Point, Ontario, Canada.

Scientific name	Common name	Occurrence status[a]	Year first observed
Agalinis purpurea	Purple false foxglove	Native	2006
Ageratina altissima	White snakeroot	Native	2021
Agrostis stolonifera	Creeping bentgrass	Exotic	2012
Anemone virginiana	Tall anemone	Native	2021
Apios americana	American groundnut	Native	2017
Apocynum androsaemifolium	Spreading dogbane	Native	2004
Apocynum cannabinum	Hemp dogbane	Native	2005
Apocynum sp.	n/a	Native	1997
Arabidopsis lyrata	Lyre-leaved rockcress	Native	2002
Arabidopsis thaliana	Mouse-ear cress	Exotic	1995
Arctostaphylos uva-ursi	Common bearberry	Native	2017
Berberis thunbergii	Japanese barberry	Exotic	2017
Bidens beckii	Water beggarticks	Native	1993
Bidens sp.	n/a	Native	2002
Bidens trichosperma	Crowned beggarticks	Native	2006
Boehmeria cylindrica	Small-spike false nettle	Native	1994
Bolboschoenus fluviatilis	River bulrush	Native	2021
Borodinia canadensis	Canada rockcress	Native	2012
Borodinia laevigata	Smooth rockcress	Native	2008
Brasenia schreberi	Watershield	Native	2021
Bromus sp.	n/a	Unknown	2017
Cakile edentula	American sea rocket	Native	1994
Campanula rotundifolia	Harebell	Native	2001
Cardamine pensylvanica	Pennsylvania bittercress	Native	1997
Carex alata	Broad-winged sedge	Native	2006
Carex albursina	White bear sedge	Native	1996
Carex bebbii	Bebb's sedge	Native	1997
Carex blanda	Woodland sedge	Native	1996
Carex buxbaumii	Buxbaum's sedge	Native	2017
Carex cephaloidea	Thin-leaved sedge	Native	2005
Carex crawfordii	Crawford's sedge	Native	2001

TABLE D1 (Continued)

Scientific name	Common name	Occurrence status[a]	Year first observed
Carex cristatella	Crested sedge	Native	2003
Carex diandra	Lesser panicled sedge	Native	1999
Carex flava	Yellow sedge	Native	1994
Carex foenea	Bronze sedge	Native	2021
Carex garberi	Garber's sedge	Native	2009
Carex gracillima	Graceful sedge	Native	2000
Carex hirsutella	Hairy green sedge	Native	2006
Carex hystericina	Porcupine sedge	Native	1995
Carex leptalea	Bristle-stalked sedge	Native	2012
Carex molesta	Troublesome sedge	Native	1997
Carex muehlenbergii	Muhlenberg's sedge	Native	1995
Carex pedunculata	Long-stalked sedge	Native	2007
Carex pellita	Woolly sedge	Native	2021
Carex prairea	Prairie sedge	Native	2011
Carex praticola	Northern meadow sedge	Native	1993
Carex pseudocyperus	Cyperus-like sedge	Native	1994
Carex rosea	Rosy sedge	Native	2012
Carex stipata	Awl-fruited sedge	Native	2009
Carex utriculata	Northern beaked sedge	Native	2004
Castilleja coccinea	Scarlet paintbrush	Native	1996
Celastrus scandens	Climbing bittersweet	Native	1993
Celtis occidentalis	Common hackberry	Native	2010
Cerastium arvense	Field chickweed	Native	2017
Ceratophyllum demersum	Common hornwort	Native	2021
Cercis canadensis	Eastern redbud	Native	2011
Chelidonium majus	Greater celandine	Exotic	2006
Circaea canadensis	Broad-leaved enchanter's nightshade	Native	2017
Cirsium muticum	Swamp thistle	Native	1995
Cirsium vulgare	Bull thistle	Exotic	1995
Clinopodium vulgare	Wild basil	Native	2003
Comandra umbellata	Bastard toadflax	Native	2009
Comarum palustre	Marsh cinquefoil	Native	2002
Conopholis americana	American cancerroot	Native	2010
Cornus obliqua	Silky dogwood	Native	2017
Cornus sericea	Red-osier dogwood	Native	1996

(Continues)

TABLE D1 (Continued)

Scientific name	Common name	Occurrence status[a]	Year first observed
Cystopteris fragilis	Fragile fern	Native	2001
Cystopteris tenuis	Mackay's brittle fern	Native	1994
Danthonia spicata	Poverty oatgrass	Native	2017
Dipsacus fullonum	Common teasel	Exotic	1993
Dryopteris carthusiana	Spinulose wood fern	Native	1998
Dryopteris cristata	Crested wood fern	Native	2009
Dryopteris intermedia	Evergreen wood fern	Native	2001
Eleocharis sp.	n/a	Native	2021
Elymus canadensis	Canada wildrye	Native	2021
Elymus hystrix	Bottlebrush grass	Native	1995
Elymus repens	Quackgrass	Exotic	2000
Elymus riparius	Eastern riverbank wildrye	Native	2001
Epilobium ciliatum	Northern willowherb	Native	2021
Epilobium coloratum	Purple-veined willowherb	Native	2003
Epilobium hirsutum	Hairy willowherb	Exotic	2000
Epilobium strictum	Downy willowherb	Native	1996
Equisetum laevigatum	Smooth scouring-rush	Native	2007
Equisetum pratense	Meadow horsetail	Native	2002
Erigeron annuus	Annual fleabane	Native	2006
Erigeron canadensis	Canada horseweed	Native	2007
Erigeron philadelphicus	Philadelphia fleabane	Native	1993
Erigeron pulchellus	Robin's-plantain fleabane	Native	2002
Euonymus atropurpureus	Eastern burning-bush	Native	2010
Euonymus europaeus	European euonymus	Exotic	2012
Eupatorium altissimum	Tall boneset	Native	2021
Fallopia convolvulus	Eurasian black bindweed	Exotic	1997
Festuca rubra	Red fescue	Exotic	1995
Festuca sp.	n/a	Unknown	1994
Festuca subverticillata	Nodding fescue	Native	1996
Fragaria virginiana	Wild strawberry	Native	2002
Fraxinus americana	White ash	Native	2021
Fraxinus pennsylvanica	Red ash	Native	2021
Galium asprellum	Rough bedstraw	Native	2005
Galium circaezans	Licorice bedstraw	Native	1995
Galium lanceolatum	Lance-leaved wild licorice	Native	2017

TABLE D1 (Continued)

Scientific name	Common name	Occurrence status[a]	Year first observed
Galium mollugo	Smooth bedstraw	Exotic	2005
Galium palustre	Common marsh bedstraw	Native	1994
Galium pilosum	Hairy bedstraw	Native	2017
Galium triflorum	Three-flowered bedstraw	Native	1994
Gentiana andrewsii	Andrews' bottle gentian	Native	2005
Geranium robertianum	Herb-robert	Native	2003
Geum canadense	Canada avens	Native	2021
Glyceria striata	Fowl mannagrass	Native	2003
Gnaphalium uliginosum	Low cudweed	Exotic	2000
Helenium autumnale	Common sneezeweed	Native	2011
Hesperostipa spartea	Plains porcupine grass	Native	2008
Hydrocharis morsus-ranae	European frog-bit	Exotic	2017
Hypericum canadense	Canada St. John's-wort	Native	2006
Hypericum majus	Large St. John's-wort	Native	2008
Hypericum punctatum	Spotted St. John's-wort	Native	1995
Ilex verticillata	Common winterberry	Native	2021
Impatiens pallida	Pale jewelweed	Native	1999
Iris versicolor	Harlequin blue flag	Native	2021
Iris virginica	Southern blue flag	Native	1993
Juncus effusus	Soft rush	Native	1993
Juncus nodosus	Knotted rush	Native	1998
Juncus tenuis	Path rush	Native	1996
Lactuca biennis	Tall blue lettuce	Native	1998
Lactuca canadensis	Canada lettuce	Native	2006
Lactuca sp.	n/a	Unknown	2021
Larix laricina	Tamarack	Native	1998
Lathyrus japonicus	Beach pea	Native	1993
Leersia virginica	White cutgrass	Native	1996
Lemna trisulca	Star duckweed	Native	2004
Leonurus cardiaca	Common motherwort	Exotic	2000
Linaria vulgaris	Butter-and-eggs	Exotic	2002
Liparis loeselii	Loesel's twayblade	Native	1993
Lithospermum canescens	Hoary puccoon	Native	1995
Lithospermum caroliniense	Golden puccoon	Native	2006
Lithospermum officinale	European gromwell	Exotic	1999

(Continues)

TABLE D1 (Continued)

Scientific name	Common name	Occurrence status[a]	Year first observed
Lolium perenne	Perennial ryegrass	Exotic	2004
Ludwigia palustris	Marsh seedbox	Native	1994
Lythrum salicaria	Purple loosestrife	Exotic	1993
Maianthemum canadense	Wild lily-of-the-valley	Native	1993
Maianthemum racemosum	Large false Solomon's seal	Native	2004
Maianthemum stellatum	Star-flowered false Solomon's seal	Native	1997
Melampyrum lineare	American cow-wheat	Native	2017
Melilotus albus	White sweet-clover	Exotic	1993
Mentha sp.	n/a	Unknown	1993
Monarda fistulosa	Wild bergamot	Native	2021
Najas flexilis	Slender naiad	Native	1999
Nasturtium officinale	Watercress	Exotic	1996
Oenothera perennis	Perennial evening-primrose	Native	2017
Onoclea sensibilis	Sensitive fern	Native	2005
Ophioglossum pusillum	Northern adder's-tongue	Native	2010
Origanum vulgare	Wild marjoram	Exotic	2012
Parthenocissus vitacea	Thicket creeper	Native	1994
Persicaria amphibia	Water smartweed	Native	1995
Persicaria hydropiper	Marshpepper smartweed	Exotic	2010
Phalaris arundinacea	Reed canarygrass	Exotic	1998
Pilosella caespitosa	Meadow hawkweed	Exotic	2002
Pinus strobus	Eastern white pine	Native	1994
Plantago major	Common plantain	Exotic	2009
Polygala polygama	Racemed milkwort	Native	2006
Polygonatum pubescens	Hairy Solomon's seal	Native	2002
Polygonatum sp.	n/a	Native	1995
Populus deltoides	Eastern cottonwood	Native	1993
Potamogeton amplifolius	Large-leaved pondweed	Native	1993
Potamogeton gramineus	Grass-leaved pondweed	Native	2005
Potamogeton illinoensis	Illinois pondweed	Native	2010
Potamogeton sp.	n/a	Native	2005
Potentilla anserina	Silverweed	Native	2003
Prenanthes sp.	n/a	Native	2021
Proserpinaca palustris	Marsh mermaidweed	Native	1995
Prunella vulgaris	Lance-leaved self-heal	Native	2007

TABLE D1 (Continued)

Scientific name	Common name	Occurrence status[a]	Year first observed
Prunus sp.	n/a	Native	1994
Quercus muehlenbergii	Chinquapin oak	Native	2021
Quercus velutina	Black oak	Native	2000
Ranunculus abortivus	Kidney-leaved buttercup	Native	2021
Rhus typhina	Staghorn sumac	Native	2021
Riccia sp.	n/a	Native	2011
Rosa multiflora	Multiflora rose	Exotic	2009
Rosa palustris	Swamp rose	Native	2002
Rosa rubiginosa	Sweetbriar rose	Exotic	2006
Rosa sp.	n/a	Unknown	2021
Rubus allegheniensis	Allegheny blackberry	Native	2002
Rubus occidentalis	Black raspberry	Native	2011
Rumex crispus	Curled dock	Exotic	2010
Rumex obtusifolius	Bitter dock	Exotic	2002
Rumex sp.	n/a	Unknown	2007
Rumex verticillatus	Swamp dock	Native	2003
Sambucus canadensis	Common elderberry	Native	2021
Schizachne purpurascens	Purple false melic	Native	2009
Scutellaria lateriflora	Mad-dog skullcap	Native	2001
Selaginella eclipes	Hidden spikemoss	Native	1994
Sisyrinchium montanum	Strict blue-eyed-grass	Native	1993
Solidago altissima	Tall goldenrod	Native	1997
Solidago caesia	Blue-stemmed goldenrod	Native	2003
Solidago canadensis complex	Canada goldenrod	Native	1998
Solidago gigantea	Giant goldenrod	Native	2021
Solidago nemoralis	Grey-stemmed goldenrod	Native	2008
Solidago ohioensis	Ohio goldenrod	Native	2002
Sonchus arvensis	Field sow-thistle	Exotic	2002
Sonchus sp.	n/a	Exotic	1996
Spirodela polyrhiza	Great duckweed	Native	2011
Stachys palustris	Marsh hedge-nettle	Exotic	2012
Stachys sp.	n/a	Unknown	2001
Stellaria longifolia	Long-leaved starwort	Native	2010
Stellaria pallida	Pale starwort	Exotic	2002
Symphyotrichum boreale	Rush aster	Native	2021

(Continues)

TABLE D1 (Continued)

Scientific name	Common name	Occurrence status[a]	Year first observed
Symphyotrichum dumosum	Bushy aster	Native	2010
Symphyotrichum ericoides	White heath aster	Native	2021
Symphyotrichum oolentangiense	Sky blue aster	Native	2017
Symphyotrichum sp.	n/a	Native	2007
Symphyotrichum urophyllum	Arrow-leaved aster	Native	2010
Teucrium canadense	Canada germander	Native	2021
Thalictrum sp.	n/a	Unknown	2021
Thlaspi arvense	Field pennycress	Exotic	2008
Thuja occidentalis	Eastern white cedar	Native	1994
Tilia americana	Basswood	Native	1995
Toxicodendron radicans	Poison ivy	Native	2008
Tragopogon dubius	Yellow goatsbeard	Exotic	2021
Tragopogon pratensis	Meadow goatsbeard	Exotic	2003
Triglochin maritima	Seaside arrowgrass	Native	1997
Trillium grandiflorum	White trillium	Native	2005
Turritis glabra	Tower mustard	Native	1996
Typha x glauca	(Typha angustifolia × Typha latifolia)	Exotic	2004
Unknown Poaceae	n/a	Unknown	2007
Unknown sp.	n/a	Unknown	2008
Utricularia gibba	Humped bladderwort	Native	2008
Utricularia intermedia	Flat-leaved bladderwort	Native	2021
Utricularia resupinata	Northeastern bladderwort	Native	1995
Utricularia subulata	n/a	Unknown	2005
Verbena hastata	Blue vervain	Native	2005
Verbena urticifolia	White vervain	Native	2003
Veronica arvensis	Corn speedwell	Exotic	1996
Veronica peregrina	Purslane speedwell	Native	2008
Veronica persica	Bird's-eye speedwell	Exotic	1996
Veronica scutellata	Marsh speedwell	Native	2003
Veronica serpyllifolia	Thyme-leaved speedwell	Exotic	2021
Viola cucullata	Marsh blue violet	Native	2004
Viola rostrata	Long-spurred violet	Native	2011
Wolffia columbiana	Columbia watermeal	Native	2017

[a]Occurrence status refers to whether a species is considered native, exotic, or of unknown distribution in Ontario, adapted from the Natural Heritage Information Centre (2021).

FIGURE D1 Photograph taken June 2022 of the long-lasting impact of deer browse effects on a stem of eastern red cedar at Long Point, Ontario, Canada. Photograph shows a browsed eastern red cedar stem with indication of a browse line at approximately 2 m above the ground, with more recent regeneration evident below 2 m. Photo by Joshua K. Pickering.