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Changes in Understory Composition of Rural North American Temperate Forests after a 14-Year Period with Focus on Exotic and Sensitive Plant Species

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Abstract: A better understanding of the mechanisms influencing compositional changes in understory plant communities is crucial to protect temperate forests against global change stressors, including anthropogenic disturbances and invasion by exotic species. We assessed changes in species composition after a 14-year period in 20 rural temperate forest stands located in the northern hardwood biome of eastern Canada. We identified species that underwent the largest changes in relative occurrence during that period and assessed the influence of biotic and anthropogenic filters on the trajectory of those understory communities. We found small but significant compositional changes after 14 years, mostly related to a decrease in species diversity in the younger forest stands originating from abandoned pasture. The largest occurrence gains for understory species were observed in these stands, but also in stands with lower understory community diversity. Understory species occurrence losses could not be linked to any of the biotic and anthropogenic filters considered in this study presumably because they were difficult to isolate from secondary successional dynamics. Shade tolerant exotic species showed a small but significant increase in relative occurrence over 14 years, with notable gains in only a few stands. We observed generalized occurrence gains for sensitive spring geophytes during the same period throughout most sites. Overall, the understory vegetation community of rural temperate forests in this region was found to be relatively stable and seems to retain its potential for natural recovery after disturbance.

Keywords: biotic and anthropogenic filters; community assembly dynamics; invasive plant species; northern hardwood biome; spring geophytes; understory flora



Citation: Bellerose, J.; Dupuch, A.; Aubin, I. Changes in Understory Composition of Rural North American Temperate Forests after a 14-Year Period with Focus on Exotic and Sensitive Plant Species. *Forests* **2022**, *13*, 678. <https://doi.org/10.3390/f13050678>

Academic Editor: Luis González

Received: 23 March 2022

Accepted: 25 April 2022

Published: 28 April 2022

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1. Introduction

Temperate forests are rich and diverse ecosystems found in several parts of the world, and are of major social and economic importance to humans [1]. As such, numerous studies have been conducted in recent decades to better understand community assembly dynamics in their understories [2]. Temperate forests harbor a high level of diversity, as reflected by the broad range of life history strategies and physiological, morphological and phenological traits that characterize their plant communities [3]. In these communities, we find numerous long-lived specialists adapted to survive in highly shaded growing conditions, although opportunistic, short-lived generalists also occur in canopy gaps following disturbance [4]. In many regions, temperate forests have been impacted by an intricate and complex land use history that may include centuries of various disturbance events [5]. As a result, many questions still remain concerning the ecological integrity of temperate forests and the potential impacts of global change stressors like climate change, habitat loss or invasion by exotic species on understory composition trajectory [1,2].

Reflecting this complexity, the mechanisms known to affect understory composition in temperate forests are numerous and diverse [2,6]. The structure and diversity of an understory plant community can act as a biotic filter and affect community composition, mostly through competition for space and resources [7]. On that matter, some studies on invasions by exotic species have showed that more diverse and dense plant communities resist changes in species composition better than sparse, less diverse plant communities, as is theorized by the biotic resistance hypothesis [8]. This theory suggests that highly diverse and dense understory communities have fewer vacant ecological niches for non-native exotic species to occupy. This theory has been tested in various types of plant communities with varying success [8]. The structure and diversity of the forest canopy can also influence understory composition [9]. Canopy gaps created by natural tree senescence, by wind or ice storm events, or by anthropogenic disturbances can increase the amount of light that reaches the ground, creating favorable conditions for increases in understory vegetation [10]. On the other hand, higher diversity and occurrence of late successional tree species such as sugar maple (*Acer saccharum* Marshall) creates a dense forest canopy in comparison with forest canopies dominated by early successional tree species (e.g., trembling aspen, *Populus tremuloides* Michaux), limiting light transmission and therefore niche space availability [11].

North American temperate forests are located in densely populated areas, and anthropogenic disturbances have profoundly affected understory community composition over time [5]. Some types of land use like maple syrup production include common management practices such as removal of non-maple saplings that have been known to reduce the structural diversity and the tree species richness of temperate forest stands, which decreases understory community diversity compared to undisturbed forests [12]. Additionally, other types of land use like wood harvesting can lead to more drastic compositional changes by opening up the canopy and disturbing the soil, facilitating the invasion of competitive plant species [13]. Past forest conversion for agricultural purposes (such as crops or pasture) can also have long-lasting impacts on understory composition [14]. Previous work noted that myrmecochorous and barochorous species were less present in reforested sites originating from abandoned farmland [15]. Changes in understory abiotic conditions caused by these disturbances can alter species composition, but also the structure of the understory by favoring the development of a dense shrub layer [16,17]. Forest fragmentation also reduces the effective dispersal of large seeded species, such as spring geophytes, while creating propagule pressure from competitive species not typically found in forests [18]. Spring geophytes are slow colonizing species found throughout North American temperate forests and are particularly sensitive to anthropogenic disturbances [3,13,16]. As such, previous work showed that these understory species can serve as indicators of ecological integrity in temperate forest stands under the influence of human activities [16].

Furthermore, anthropogenic disturbances can facilitate the establishment and expansion of introduced exotic species because they are able to benefit from the sudden availability of niche space [19]. The invasion potential of exotic plant species in temperate forests can vary considerably depending on species' autecology. Despite this variation, several studies noted that successful invaders in temperate understories are most often shade tolerant species with considerable leaf plasticity and regeneration capacities [20–22]. These exotic species are of particular concern for North American temperate forests, as they can still thrive in the low light conditions of the understory while also being able to rapidly exploit resources following disturbance [20]. Evidence of competition for space and resources was observed between those shade tolerant trees or shrubs and native tree species in several understory communities of North American temperate forests [21,23]. For example, many studies on forest invasions in the eastern United States have reported cases of rural forest understories invaded by shade tolerant exotic shrubs (e.g., Chinese privet, *Ligustrum sinense* Loureiro; Japanese honeysuckle, *Lonicera japonica* Thunberg; European buckthorn, *Rhamnus cathartica* L.), impacting local understory community composition and structure [21,22]. Some shade tolerant exotic herbs are also considered threats for North

American forests. For instance, garlic mustard (*Allaria petiolata* (M. Bieberstein) Cavara & Grande) can have a strong allelopathic effect which limits germination success [24] as well as reduces colonization by mycorrhizae on the roots of native herbaceous species [25]. As such, the occurrence of shade tolerant exotic species and their potential impact on the local flora of North American temperate hardwood forests need to be more closely analysed in conjunction with the monitoring of sensitive forest species such as the spring geophytes.

Due to logistical constraints, most studies examining changes in understory community composition in temperate forests used a space-for-time approach (i.e., chronosequence) [26]. Although adequate to assess contrasted responses, this experimental design limits our capacity to differentiate between different mechanisms of community assembly that can lead to similar spatial patterns, increasing the likelihood of inferring incorrect conclusions with the available data [26,27]. Without long-term monitoring of forest stands over multiple surveys, detecting local changes in species composition and plausibly inferring the underlying understory community assembly dynamics remain a challenge that chronosequence studies alone cannot reasonably overcome [28].

In this study, we assessed understory plant community composition changes after a 14-year period in a set of temperate deciduous forest stands situated in a rural region of the northern hardwood biome of eastern Canada. These forests have been subjected to numerous anthropogenic pressures over the years, and several exotic species are present in the area. Many native sensitive spring geophyte species threatened with local or regional extinction (e.g., Wild leek, *Allium tricoccum* Aiton and American ginseng, *Panax quinquefolius* L.) [29] are known to occur in these habitats. These forests have a complex land use history [30], stand structure and understory conditions [16]; the region is thus an ideal area to evaluate changes in species composition in understory plant communities of rural temperate forest ecosystems. Resurveying after 14 years provides an opportunity to deepen our understanding of the mechanisms behind understory composition changes. We first evaluated changes in the plant species composition and diversity at each study site after 14 years. This allowed us to identify which plant species have undergone the most important changes in terms of relative occurrence (either occurrence gains or losses; Q1). To understand what drives these variations, we looked at which biotic and anthropogenic filters had the most influence on changes in species' relative occurrence (Q2). Finally, we assessed if shade tolerant exotic species with high invasion potential have shown occurrence gains after 14 years in our region (Q3) and if sensitive spring geophytes have seen a decline in their relative occurrence during the same time period (Q4).

2. Materials and Methods

Data were collected in the Great Lakes-St-Lawrence forest region of southern Quebec, Canada, in the Upper Saint-Lawrence Valley (45°01'–45°08' N, 73°58'–74°21' W). Mean annual temperature in the area is 5 °C, total annual precipitation ranges from 900 to 1000 mm and the growing season typically lasts 190–200 days [31]. Mature mesic forests in the region are dominated by sugar maple, which co-occur with many species like bitternut hickory (*Carya cordiformis* (Wangenheim) K. Koch), eastern hop-hornbeam (*Ostrya virginiana* (Miller) K. Koch), black cherry (*Prunus serotina* Ehrhart) and basswood (*Tilia americana* L.) [32]. White ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), trembling aspen and grey birch (*Betula populifolia* Marshall) are typically found on disturbed sites [33]. Small gaps created by tree senescence are characteristic of the natural disturbance regime of the region, while some large scale disturbances such as ice storms and wind throw occur occasionally [31]. At the beginning of the 19th century, most of the land suitable for agriculture was deforested and converted to grow crops or to be used as pasture [30]; only forests unsuitable for agriculture were kept intact and used for firewood and maple syrup production [32]. During the 20th century, a proportion of these marginal farmlands was abandoned and left to regenerate naturally [30], while agricultural lands are now concentrated in the nutrient-rich marine clays deposits of the St-Lawrence lowlands [31].

We resurveyed twenty stands in 2017 that were previously assessed in 2003 by Aubin et al. [16], because of their spatial proximity, their lack of major recent changes in forest structure linked to human activities, and their accessibility in the summer of 2017. These stands were chosen to represent the broad range of anthropogenic land uses that occurred over the last century and were divided in three different types of forest structure frequently found in the region (Table 1). Signs of disturbance were classified into three main categories: maple syrup production, partial wood harvesting and abandoned pasture. Syrup production stands were easily identified by the presence of sap-collecting tubes, while partially harvested stands were identified by the presence of tree stumps and skid trails. Vegetation dynamics after pastoral and agricultural activities have been studied extensively in the region [30]. These studies were used to identify stands originating from the abandonment of pasture by noting at least one visible sign of past agricultural use (e.g., fence or large tree with a broad, open-grown crown). Year of land abandonment and land use history were later validated through aerial photograph interpretation (1964–1966, 1975–1983). Stands without recent human disturbance had no visible signs of pasturing, tree harvesting or other human activities, either in the field or on aerial photographs. We assumed these stands had no human disturbances of importance during the second part of the 20th century. These past land use signs were evaluated during the summer 2003 by Aubin et al. [16]. Fourteen years later, the same inventory of past land use signs was repeated in the same twenty stands during the summer 2017 to assess the changes in recent disturbance history.

Table 1. Characteristics of the 20 study stands divided in three different types of forest structure commonly occurring in the region. Value ranges are shown for stand age, and average values are shown for basal area and stem density.

Forest Structure	N	Stand Age in 2017	Characteristics	Basal Area (m ² ha ^{−1})	Stem Density (N ha ^{−1})
Mature maple (MM)	13	>70 years old	Mature canopy dominated by maple trees	24.6	600
Immature maple (IM)	3	35–50 years old	Closed canopy dominated by young maple trees	21.5	550
Reforested (RF)	4	25–45 years old	Closed canopy originating from abandoned pasture	18.8	1018

Understory vegetation inventories were conducted in 2003 and 2017 following the same protocol (see [16] for more details). In both sampling years, inventories were conducted in May, July and September to capture all plant species present over the course of a growing season. All plants (225 species present in at least one or both inventories) were identified to species except for serviceberries (*Amelanchier* Medikus), sedges (*Carex* L.), field bindweeds (*Convolvulus* L.), hawthorns (*Crataegus* L.), strawberries (*Fragaria* L.), white lettuces (*Nabalus* Cassini), roses (*Rosa* L.), and willows (*Salix* L.), which were identified to genus, and grasses (*Poaceae* Barnhart) which were identified to family. All woody species with a diameter at breast height (DBH) < 5 cm were included. Each species was categorized as native (187 species) or exotic (38 species) using previous studies [34–37] and flora of eastern North America [38]. Plot centers for the 2017 inventories were determined using GPS coordinates and were within a 5 m distance from the plot centers of the 2003 inventories. Vegetation inventories were conducted in 2000 m² (0.2 ha) plots along four 25 m linear transects in each cardinal direction. Vascular species were systematically sampled in circular points (15 cm radius) every 2 m, starting at the 1 m mark (13 points per transect). Species within a sampling point were given an occurrence value of 1, and then summed across all sampling points, for a total possible score of 52. Species present within the 2000 m² plot but not at any of the sampling points, were assigned a total occurrence score of 0.5. The relative occurrence of a given species was calculated as the proportion of occurrence points within a plot (i.e., total occurrence score divided by 52, in %) where that species occurred.

Using data from the vegetation inventories, four biotic variables were calculated in each plot to evaluate the influence of the diversity and structure of the understory layer and forest canopy on community composition dynamics (Table 2). The Shannon–Wiener index was calculated from the matrices of species relative occurrence for each inventory year ($H'03/H'17$), using the following formula:

$$H' = - \sum_{i=1}^R p_i \ln p_i \quad (1)$$

Table 2. Description of the biotic and anthropogenic variables measured or calculated at each stand, as well as the underlying filter associated to each variable.

Variable Name	Units	Description	Filter
Biotic variables			
$H'03/H'17$	-	Shannon–Wiener index for species richness of the entire understory plant community, calculated separately for the 2003 ($H'03$) and the 2017 ($H'17$) inventories	Understory structure and diversity
Cover	%	Relative proportion of sampling points (52 in total) with at least one occurring species	Understory structure and diversity
BArea	m ² /ha	Basal area per hectare of late successional tree species with DBH > 5 cm	Canopy structure and composition
Open	%	Relative proportion of canopy openness based on 52 sampling points (open—1 point; semi-open—0.5 point; closed—0 point)	Canopy structure
Anthropogenic variables			
Maple	Binary	Maple syrup production: 0—Never recorded since 1964, 1—Recorded at least once in 2003 or still ongoing	Disturbance—minor intensity
UndCut	Binary	Recent clearing of undergrowth vegetation: 0—Never recorded since 2003, 1—Recorded at least once in 2003 or 2017	Disturbance—minor intensity
ParCut	Binary	Partial wood harvesting: 0—Never recorded since 1964, 1—Recorded at least once in 2003 or 2017	Disturbance—major intensity
Graze	Ordinal	Pastureland grazing: 0—Never recorded since 1964, 1—Recorded at least once between 1964 and 1975, 2—Recorded at least once between 1975 and 2003 but not in 2017	Disturbance—major intensity
Age	Years	Time since last anthropogenic disturbance	Disturbance frequency
Anth	%	Relative proportion of surrounding lands with anthropogenic activities evaluated with regional satellite maps in 2017	Fragmentation and habitat loss

Total understory plant cover was calculated using the relative proportion of sampling points where at least one species was present in 2017 (Cover). Canopy composition was characterised for the 2017 inventory year based on the basal area of late successional tree species only (see Table S1 for species list) and for stems with a DBH > 5 cm (BArea). Furthermore, forest canopy opening was assessed at each sampling point during the 2017 inventory using a semi-quantitative metric of openness (i.e., open—1 point; semi-open—0.5 point; closed—0 point). From here, we estimated canopy openness based on the sum of openness scores proportional to all points assessed in a given plot (in %; Open).

Six anthropogenic variables linked to land use history were assessed at each plot using past/current observations and satellite imagery to evaluate the influence of disturbance intensity/frequency, landscape fragmentation and habitat loss on community composition dynamics (Table 2). We created three binary variables and one ordinal variable using information from the previous study [16] to characterize both past and present land use activities that have occurred over the last 70 years in each plot (i.e., maple syrup production (Maple), understory vegetation clearing (UndCut), partial wood harvesting (ParCut) and pasture/grazing (Graze)). These human activities have been identified during extensive

studies in the region as the main land uses that occur in these forests throughout the last century or so (see [30] for more details). The stand age, i.e., time since the last disturbance from these aforementioned activities, was also estimated based on past/current observations and aerial photographs (Age). Additionally, the relative proportion of surrounding anthropogenic landscapes in 2017 (i.e., housing, farming, roads, etc., in a 2 km radius) was calculated using regional satellite maps and Google Earth (Anth).

To evaluate changes in the understory community diversity at each study site over time (Q1), we tested for differences in Shannon–Wiener index values between 2003 and 2017 using a Wilcoxon paired *t*-test analysis for non-normal data [39] as implemented in R version 3.5.1 [40] (*wilcox.test* function in the *stats* package). We also performed a nested PERMANOVA analysis [41] on the matrices of species relative occurrences to estimate changes in the understory community composition between 2003 and 2017 (*adonis* function in the *vegan* package in R). From here, we identified plant species that underwent the greatest changes in relative occurrence between inventories. To do this, we used a species-centered Procrustes analysis [42] to determine the degree of superimposition between the 2003 and 2017 species occurrences matrices. This analysis yielded a Procrustes residual value for each plant species, representing their absolute magnitude of change in occurrence between inventories. Species with a Procrustes residual value \geq 80th percentile (i.e., 20% of the observed plant species, $N = 45$) underwent the greatest changes in relative occurrence over time, and were classified based on whether they increased ($N = 24$; species with the largest gains hereafter) or decreased ($N = 21$; species with the largest losses hereafter). This analysis was done using the *procrustes* function in the *vegan* package in R.

To evaluate the influence of biotic and anthropogenic filters on understory community composition changes over time (Q2), we first conducted two forest stand-centered Procrustes analyses to determine the degree of superimposition between 2003 and 2017, using sub-matrices for species with the largest gains and losses in relative occurrence, respectively. This allowed us to obtain two Procrustes residual values for each stand, each representing the absolute magnitude of local community gains and losses that occurred during the 14-year period. Two different multiple regression analyses [43] were conducted using the two stand-level Procrustes residual values as dependent variables and stand-level filters (Table 2) as independent variables. Regression analyses were conducted using the *lm* function in R, and the model with the lowest AICc (Akaike Information Criterion adjusted for sample size) was selected as the best regression model [44]. When multiple models were within two units of the lowest scoring model, we selected the most parsimonious model (i.e., with the smallest number of parameters).

To assess if the relative occurrence of shade tolerant exotic species (Q3) and sensitive spring herbaceous geophyte species (Q4) changed over time, we compared each group's relative proportion in stand total occurrences as found in the 2003 and 2017 inventories, using a Wilcoxon paired *t*-test for non-normal data [39]. The first group included 11 shade tolerant exotic species identified as potentially invasive in previous studies [34,35] and that were present in at least one inventory (see Table S2 for species list). The second group included 34 spring herbaceous geophyte species that were identified in the literature as sensitive to forest disturbances [13] and that were present in at least one of our inventories (see Table S3 for species list). Certain known sensitive taxa identified in previous studies (e.g., a mycoheterotrophic species, Indian pipe *Monotropa uniflora* L. [45]), could not be included in our analysis due to their low overall occurrence (five species representing 0.08% of the total vegetation inventory over both years). To verify if a decline in spring geophytes species could be associated with expansions of shade tolerant exotic species, we conducted a Spearman correlation analysis for non-normal data [46] based on the variation of relative proportion in stand total occurrences over 14 years ($\Delta\%_{AVG}$) for both groups. This analysis was done using the *cor* function in the *stats* package in R.

3. Results

3.1. Changes in Community Diversity and Composition after 14 Years (Q1)

We detected a significant decrease in understory species diversity in the study sites between 2003 (Shannon–Wiener index \pm S.E. = 2.90 ± 0.33) and 2017 (Shannon–Wiener index \pm S.E. = 2.76 ± 0.30) (Wilcoxon paired t -test: $N = 20$, $p = 0.032$), as well as a small but significant change in plant community composition (PERMANOVA: $N = 20$, $df = 39$, $F = 3.03$, $R^2 = 0.07$, $p = 0.001$). The most important decrease in understory diversity after 14 years was found in the reforested stands originating from abandoned pasture, while changes in diversity observed in mature and immature maple stands were smaller in magnitude and more nuanced (Figure 1). Among species that underwent the greatest changes in relative occurrence between 2003 and 2017 (Table 3), broad-leaved enchanter’s nightshade (*Circaea canadensis* (L.) Hill) showed the greatest changes in occurrence when subgroups were considered, in terms of variation of the average values of the species’ relative proportion in stand total occurrences “ $\Delta\%_{AVG}$ ” (gains: $\Delta\%_{AVG} = 12.79\%$, $N = 10$; losses: $\Delta\%_{AVG} = -10.44\%$, $N = 7$; no changes: $N = 2$; Table 3). However, the variation in this species’ relative proportion in total vegetation occurrences across all stands “ $\Delta\%_{TOT}$ ” was low ($\Delta\%_{TOT} = 0.98\%$, $N = 19$). When changes in relative proportion across all sites were considered, yellow trout lily (*Erythronium americanum* Ker Gawler) had the largest gains ($\Delta\%_{TOT} = 7.3\%$, $\Delta\%_{AVG} = 8.12\%$, $N = 18$), while sugar maple showed the greatest losses ($\Delta\%_{TOT} = -11.0\%$, $\Delta\%_{AVG} = -11.67\%$, $N = 20$).

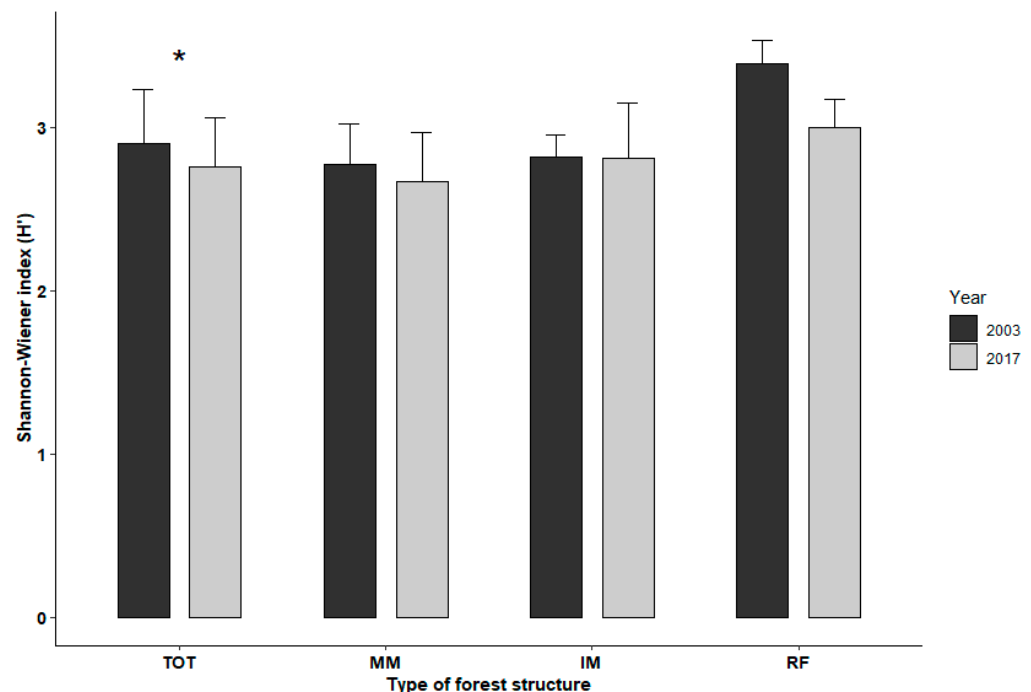


Figure 1. Bar graph comparing average Shannon–Wiener index (H') values of understory plant communities, calculated for each type of forest structure between the 2003 and 2017 inventories, with standard deviation (SD) depicted as error bars. TOT: total ($N = 20$); MM: mature maple ($N = 13$); IM: immature maple ($N = 3$) RF: reforested ($N = 4$). Significant differences between average index values for each year (i.e., $p < 0.05$), as evaluated by the Wilcoxon paired- t test analysis, are noted by an asterisk (*). No statistical test was conducted on the immature maple and the reforested stands because of their insufficient sample size.

Table 3. Comparison of average values and standard deviation (SD) of the relative proportion in stand total occurrences (%AVG) between the 2003 and 2017 inventories of understory communities for species that underwent the largest (A) gains or (B) losses of occurrence. Each species' relative proportion in the total vegetation across stands (i.e., all 20 study sites combined; %TOT) for both years and Procrustes residual value are also represented. Only species with a Procrustes residual value \geq 80th percentile are shown (see Table S4 for list of all plant species).

Species	2003			2017			Procrustes Residuals
	%TOT	%AVG	SD	%TOT	%AVG	SD	
A. Occurrence gains (24 species)							
<i>Circaea canadensis</i>	2.2	2.44	2.59	3.6	3.42	5.41	54.71
<i>Erythronium americanum</i> ¹	6.6	6.18	7.38	13.9	14.3	12.1	51.89
<i>Ostrya virginiana</i>	5.9	5.84	5.51	6.4	5.89	6.46	48.80
<i>Carya cordiformis</i>	1.7	1.81	1.70	5.1	5.79	5.22	47.62
<i>Onoclea sensibilis</i>	0.9	0.51	1.63	1.7	0.86	3.21	32.00
<i>Zanthoxylum americanum</i>	1.5	1.41	2.61	1.8	1.66	2.56	31.03
<i>Trillium grandiflorum</i> ¹	4.3	4.19	6.03	5.0	4.56	6.47	27.66
<i>Cornus alternifolia</i>	1.7	1.94	3.28	2.9	2.91	3.97	27.02
<i>Dryopteris carthusiana</i>	0.9	0.95	2.18	1.6	1.80	2.63	26.03
<i>Rubus occidentalis</i>	0.4	0.39	0.91	0.9	0.79	1.75	23.03
<i>Maianthemum canadense</i>	0.8	0.74	1.12	1.4	1.42	2.09	22.84
<i>Poaceae</i> spp.	0.9	0.75	1.18	1.1	0.98	1.59	20.78
<i>Caulophyllum thalictroides</i>	2.1	2.49	4.38	2.2	3.21	7.47	19.16
<i>Thuja occidentalis</i>	0.6	0.52	1.10	0.7	0.55	1.43	19.07
<i>Prunus virginiana</i>	1.4	1.47	1.31	2.0	1.97	2.83	18.46
<i>Rubus allegheniensis</i>	0.7	0.66	1.09	0.9	0.69	1.11	18.42
<i>Polystichum acrostichoides</i>	0.5	0.42	1.18	0.6	0.51	0.78	17.10
<i>Ulmus rubra</i>	0.8	0.81	2.39	1.1	1.06	2.71	16.92
<i>Populus tremuloides</i>	0.2	0.13	0.49	0.3	0.16	0.48	16.39
<i>Parthenocissus quinquefolia</i>	0.8	0.69	1.23	1.0	0.82	1.17	16.32
<i>Rubus pubescens</i>	0.6	0.33	1.44	0.6	0.34	1.14	15.04
<i>Prunus serotina</i>	0.7	0.75	0.68	0.8	0.77	1.29	14.21
<i>Cardamine concatenata</i> ¹	0.06	0.08	0.23	0.4	0.52	1.72	13.04
<i>Athyrium filix-femina</i>	0.7	0.68	0.98	0.6	0.73	1.39	12.24
B. Occurrence losses (21 species)							
<i>Acer saccharum</i>	17.7	20.2	10.6	6.7	8.53	7.63	194.03
<i>Claytonia caroliniana</i> ¹	2.1	1.67	4.95	0.7	0.87	2.35	83.03
<i>Fagus grandifolia</i>	1.6	1.42	3.24	0.3	0.40	0.51	60.97
<i>Fraxinus americana</i>	7.4	7.48	6.38	7.8	6.96	6.52	42.19
<i>Carpinus caroliniana</i>	1.1	1.21	4.25	0.3	0.35	1.44	42.14
<i>Acer rubrum</i>	0.8	0.66	2.64	0.3	0.25	0.88	34.43
<i>Tilia americana</i>	1.6	1.65	1.96	0.5	0.55	0.61	26.15
<i>Ulmus americana</i>	1.3	1.18	1.32	0.1	0.10	0.24	25.67
<i>Rubus hispidus</i>	0.5	0.39	1.73	0.1	0.14	0.34	25.11
<i>Carex</i> spp.	3.4	3.08	2.84	3.6	2.94	2.70	23.06
<i>Rubus idaeus</i>	0.7	0.64	1.63	0.1	0.14	0.45	22.87
<i>Equisetum pratense</i>	0.4	0.37	1.61	0.2	0.16	0.60	20.30
<i>Cornus obliqua</i>	1.3	0.75	2.88	1.4	0.64	2.72	20.03
<i>Potentilla reptans</i> ²	0.3	0.15	0.69	0.02	0.01	0.04	17.73
<i>Galium palustre</i>	0.3	0.17	0.75	0.07	0.03	0.15	17.12
<i>Acer nigrum</i>	0.7	0.64	1.63	0.1	0.14	0.45	16.94
<i>Hepatica acutiloba</i> ¹	0.7	0.79	1.56	0.7	0.57	0.93	16.23
<i>Symphyotrichum lateriflorum</i> var. <i>lateriflorum</i>	0.9	0.87	1.15	0.5	0.40	0.67	15.02
<i>Vitis riparia</i>	0.8	0.83	1.05	0.7	0.74	0.78	14.44
<i>Cornus sericea</i>	0.3	0.23	0.75	0.04	0.02	0.07	13.53
<i>Solidago flexicaulis</i>	0.5	0.57	1.03	0.4	0.32	0.52	12.20

¹ Sensitive spring geophyte species; ² Shade intolerant exotic species; No shade tolerant exotic species were present in the 45 species that experienced the largest changes of occurrence over 14 years.

3.2. Identification of Biotic and Anthropogenic Filters Influencing Changes in Species Occurrence (Q2)

For species with the largest occurrence gains, model selection showed that two models were within two units of the lowest AICc value (Table 4). Since the basal area of late successional tree species (BArea) was not a significant variable, we selected the most parsimonious model.

monious model as the best model, which included time since last disturbance (Age) and Shannon–Wiener index of the understory plant community in 2017 (H'17) as explanatory variables (Table 5). This model predicts that species occurrence gains decrease as time since disturbance (Figure 2a) and understory community diversity increase (Figure 2b). For species with the largest occurrence losses, model selection showed that the null model (i.e., the model without any explanatory variables) was the best model (Table 4), suggesting that species occurrence losses were not associated with any of the estimated biotic and anthropogenic filters included in the analyses.

Table 4. Comparison of the five candidate models with the lowest corrected Akaike Information Criteria (AICc), predicting changes in occurrence for (A) the 24 species with the largest gains and (B) the 21 species with the largest losses in the study sites (Q2). The number of parameters (k), the ΔAICc and the Akaike weight (W_i) of each model are presented. The selected model is denoted by an asterisk (*).

Model	k	AICc	ΔAICc	W_i
A. Species with the largest occurrence gains				
Age + H'17 *	4	163.12	0.00	0.48
Age + BArea + H'17	5	164.54	1.42	0.24
Age + Open + H'17	5	166.30	3.19	0.10
Age + Anth + H'17	5	166.31	3.19	0.10
Age + UndCut + H'17	5	166.48	3.37	0.08
B. Species with the largest occurrence losses				
Null *	2	171.68	0.00	0.31
Age	3	172.33	0.65	0.23
Age + ParCut	4	172.54	0.86	0.20
Maple	3	173.18	1.50	0.15
Age + UndCut	4	173.86	2.18	0.11

Table 5. Outputs of the best model explaining changes in occurrence for species with the largest gains ($N = 24$) in relation to time since last disturbance (Age) and Shannon–Wiener index of the understory plant community diversity in 2017 (H'17). The adjusted coefficient of determination (R^2_{adj}) and the p -value of the best model are shown, as well as the estimate (\pm standard error), the Student's t value and the p -value of each variable.

Variable	R^2_{adj}	Estimate (\pm SE)	t Value (df = 17)	p
Model	0.31			0.017
Intercept		129.3 (\pm 32.6)	3.97	<0.001
Age		−0.42 (\pm 0.16)	−2.66	0.016
H'17		−30.1 (\pm 10.4)	−2.89	0.01

3.3. Detecting Occurrence Changes for Shade Tolerant Exotic Species (Q3) and for Sensitive Spring Geophytes (Q4) after 14 Years

Across study plots, we recorded seven shade tolerant exotic species in 2003 compared to ten in 2017, and observed that they represented a slightly higher relative proportion of the total vegetation across stands (i.e., all 20 study sites combined) in 2017 ($\%_{\text{TOT}} 2003 = 1.6\%$ vs. $\%_{\text{TOT}} 2017 = 2.4\%$; Table 6). We also detected a small but significant increase in the average value of their relative proportion in the understory community of each stand between both years ($\Delta\%_{\text{AVG}} = 1.92\%$, $p = 0.040$; Table 6), with notable expansions in only a few stands. Similarly, the relative proportion of sensitive spring herbaceous geophytes in the total vegetation across stands increased between 2003 ($\%_{\text{TOT}} = 20\%$) and 2017 ($\%_{\text{TOT}} = 27\%$), although a similar number of species were recorded (2003: $N = 31$; 2017: $N = 30$; Table 6). We detected a significant increase in their average relative proportion across sites in the understory community of each stand over time ($\Delta\%_{\text{AVG}} = 10.3\%$, $p < 0.001$; Table 6). Finally, we did not find any evidence of declines in sensitive spring geophytes caused

by the expansion of shade tolerant exotic species in our study sites (Correlation: $N = 20$, $\rho_{\text{Spearman}} = 0.02$, $t_{18} = -0.59$, $p = 0.563$).

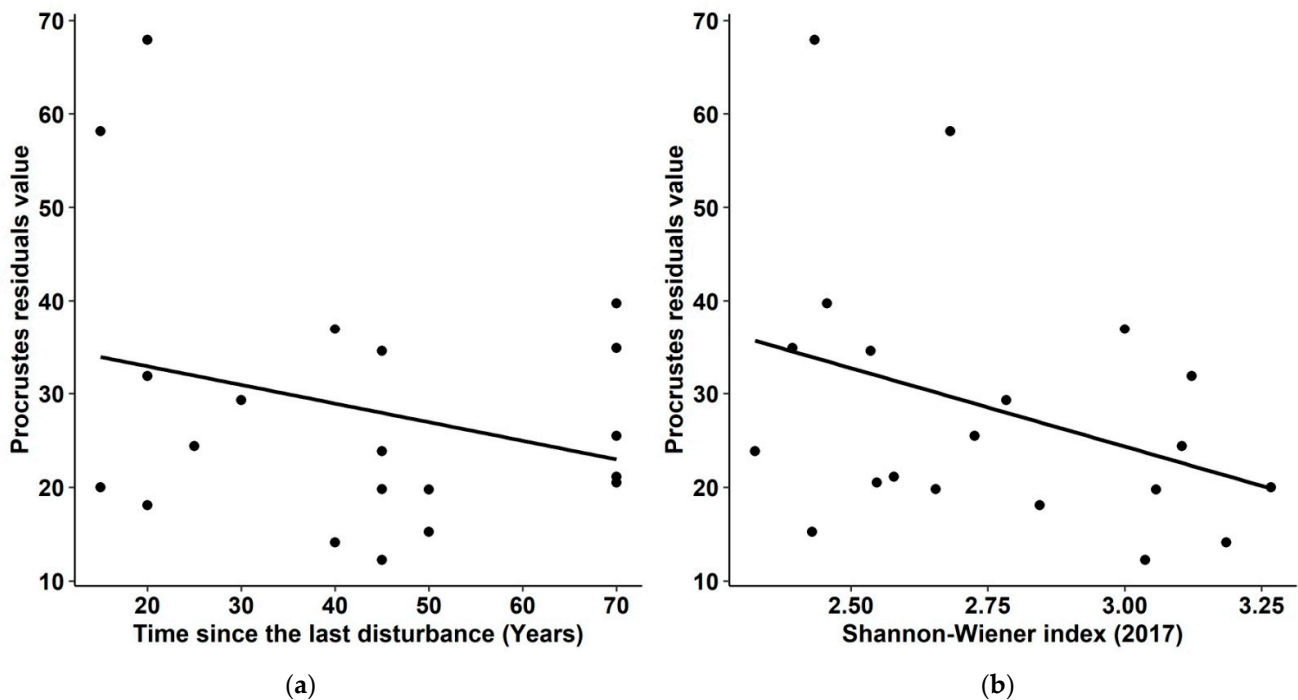


Figure 2. Results of the multiple linear regression analysis between the stand-centered Procrustes residual values representing the magnitude of changes in occurrence for species with the largest gains between 2003 and 2017 ($N = 24$) and the two explanatory variables revealed by multimodel selection (Q2), i.e., (a) the time since the last disturbance (Age) and (b) the Shannon–Wiener index of the understory plant community in 2017 (H'_{17}). The fitted regression model lines (Age: $y = 129.3 - 0.42x$; H'_{17} : $y = 129.3 - 30.1x$) are shown for each explanatory variable.

Table 6. Comparison of average values and standard deviation (SD) of the relative proportion in stand total occurrences ($\%_{\text{AVG}}$), for shade tolerant exotics (Q3) and sensitive spring geophytes (Q4) between the 2003 and 2017 understory communities inventories ($N = 20$). Statistics of the Wilcoxon paired t -test (direction of changes and associated p -value) are also included, as well as the number of species (N_{Sp}) in each group and their relative proportion in the total vegetation across stands (i.e., all 20 study sites combined; $\%_{\text{TOT}}$) for both years (see Tables S2/S3 for species list).

Group	2003				2017				Direction	p
	N_{Sp}	$\%_{\text{TOT}}$	$\%_{\text{AVG}}$	SD	N_{Sp}	$\%_{\text{TOT}}$	$\%_{\text{AVG}}$	SD		
Shade tolerant exotics	7	1.6	1.88	3.60	10	2.4	2.80	5.46	Gain	0.040
Sensitive spring geophytes	31	20	19.8	13.7	30	27	30.1	17.9	Gain	<0.001

4. Discussion

In this study, we assessed changes in the understory composition after a 14-year time period in temperate forest stands located in the northern hardwood biome of eastern Canada. This area has a complex history of land use and is under threat of invasion by several exotic plant species, which may impact its future ecological integrity. Our analyses showed significant but small changes in understory community composition over this time period, as well as a decrease in species diversity mainly associated with reforested stands originating from abandoned pasture. Although we noted significant gains in relative occurrence for shade tolerant exotic species in a few study sites, we also observed occurrence gains for sensitive spring geophyte species throughout most of the stands.

The changes in understory composition we observed after 14 years agree with other studies conducted in the northern hardwood biome [47,48]. For example, Woods et al. [47] noted a decrease in stand-scale understory diversity over 30 years in Wisconsin, U.S.A., even though no species losses were observed and total herbaceous cover increased. They concluded that these small-scale changes in understory composition were probably driven by competition and local changes in canopy composition, as explained by gap dynamics theory [49]. In our case, the most important changes in understory composition were observed in the reforested sites. Other studies in abandoned pasturelands also found high diversity levels coupled with compositional changes over time related to secondary succession mechanisms [50]. These succession mechanisms may also explain the composition changes we observed in our reforested stands. In comparison, limited compositional changes were found in mature maple stands over the course of our study. In these stands, the most important changes were related to the occurrence of tree seedlings, presumably influenced by seed mast years [51]. Seedling occurrence may also have been affected by an important drought in 2012 [52] or by over-browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann) [53]. Nevertheless, our results still support the finding that mature temperate forests usually undergo fewer compositional changes.

The species that underwent the largest occurrence gains after 14 years included herbs with high dispersal abilities (e.g., broad-leaved enchanter's nightshade) and shrubs with high competitive ability (e.g., northern prickly-ash, *Zanthoxylum americanum* P. Miller; Allegheny blackberry, *Rubus allegheniensis* Porter), but also seedlings of certain tree species (e.g., bitternut hickory) and some sensitive spring geophytes (e.g., white trillium, *Trillium grandiflorum* (Michaux) Salisbury; yellow trout lily). The species that experienced the greatest occurrence losses over this period included seedlings of late successional trees (e.g., sugar maple; American beech, *Fagus grandifolia* Ehrhart), spring geophytes (e.g., Carolina spring beauty, *Claytonia caroliniana* Michaux), shade intolerant shrubs (e.g., red raspberry, *Rubus idaeus* L.; silky dogwood, *Cornus obliqua* Rafinesque) and some other herb species (e.g., common marsh bedstraw, *Galium palustre* L.; creeping cinquefoil, *Potentilla reptans* L.). Northern hardwood understory species possess a wide range of strategies to maintain themselves under a deciduous canopy, from slow-growing understory specialists [54] to competitive ubiquitous species with high levels of plasticity in response to canopy opening [55]. A 50-year temporal survey conducted in forested stands in Wisconsin and Michigan, U.S.A. observed an increase in the occurrence of widespread native generalists and exotic species as well as a decrease in native forest specialists [56]. Although the disappearance of forest specialists in disturbed stands of North American temperate forests over recent decades is well documented [15,57], we did not observe such trends in our rural study sites. For instance, the occurrence of spring geophytes, an indicator group of specialist species known to be sensitive to disturbances [13], increased in our stands over 14 years. Interestingly, the most important gains in this group were observed in our reforested sites and younger maple stands, and can largely be attributed to the colonization of yellow trout lily and white trillium. Since these two long-lived perennials are slow growing [58,59] and mostly rely on ants for seed dispersal [60,61], we believe that the occurrence gains we observed in these stands come mainly from the reproduction of individuals that survived disturbance (and deforestation) in hedgerows and shrub thickets [62,63].

Species with the largest occurrence gains increased mainly in younger stands (both immature maple and reforested stands) with lower understory community diversity. These results support the biotic resistance hypothesis [8], which suggests that understory communities with lower species diversity are more vulnerable to rapid expansions of competitive species compared to highly diverse communities with few vacant niches. Future surveys will be needed in this region to document the vulnerability of local temperate stands to exotic plant invasions, since previous work noted that biotic resistance can slow down the establishment of invaders, but not completely stop them [64]. However, we could not associate any of the filters considered in this study to declines in species occurrence in our

study sites, although we believe this may be partly attributed to successional processes associated with reforested stands [50]. Previous work [65] showed regional variation in land use history to be related to biophysical characteristics, which also affects the natural processes of understory communities. These confounding factors make it difficult to disentangle the effects of the different mechanisms guiding understory community assembly dynamics in temperate forests.

We observed a small but significant increase in shade tolerant exotic species over 14 years, mainly due to an increase in the relative occurrence of European buckthorn. Although already present in 50% of our sites in 2003, notable occurrence gains for this species were limited to a few younger sites, mainly reforested sites and immature maple stands. As such, we did not find substantial evidence of invasion by shade tolerant exotic species in our study sites. European buckthorn is a persistent shade tolerant shrub with considerable leaf plasticity and regeneration capacities [66]. It was introduced in North America in the late 19th century for medicinal purposes, but rapidly escaped from gardens and became naturalized in most of the northeastern part of the continent over time [23]. Its invasion in numerous urban woodlands has been broadly documented in recent years (e.g., [23]). Our results thus contrast sharply with the findings of these studies, since we observed a much slower rate of expansion of buckthorn populations in our study sites over 14 years. More monitoring is needed to better understand why our rural sites seem to limit buckthorn invasions better than urban woodlands. Comparative studies with other regions experiencing exotic plant invasions may also provide insights on the mechanisms governing the expansion of exotic species (e.g., colder climate or more recent introduction in our region compared to southern hardwood forests) [21,22]. Biological invasions are frequently studied after the fact, and our study exemplifies the importance of establishing local long-term monitoring plots to detect future invasions early.

Contrary to studies conducted in other North-American temperate forests [15,57], our results hint towards an overall resilience of mature stands in these rural temperate forests, even in stands that have faced a variety of anthropogenic disturbances in the past. Our results also show that abandoned pasturelands in the region have the potential to recover naturally while being more susceptible to invasion by exotic plants than mature stands. In contrast with studies done in the temperate forests of the eastern United States [67,68], our analyses did not show any declines in understory specialists associated with the expansions of exotic species in our study sites. Studies over longer periods like this one allow the monitoring of small local changes that could help deepen our understanding of the mechanisms behind exotic species invasions, but also behind the resilience of sensitive forest specialist species under anthropogenic pressure. We believe that such studies are necessary to better anticipate the effects of global changes stressors on temperate forest understory communities in the coming decades.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f13050678/s1>, Table S1: List of late successional tree species identified and measured at least once in the study sites (DBH > 5 cm) and used to calculate basal area (Table 2; BArea); Table S2: List of shade tolerant exotic species identified at least once in the study sites along with their region of origin, introduction date in the study region and degree of invasiveness in Canada (Q3; Table 6; Shade tolerant exotics); Table S3: List of sensitive spring geophyte species identified at least once in the study sites (Q4; Table 6; Sensitive spring geophytes); Table S4: Changes in average values and standard deviation (SD) of the relative proportion in total stand occurrences (%_{AVG}) between the 2003 and 2017 inventories of understory communities for all species identified at least once in the study sites and categorized depending on the direction of change (i.e., occurrence (A) gains or (B) losses).

Author Contributions: Conceptualization, J.B., A.D. and I.A.; methodology, J.B., A.D. and I.A.; software, J.B.; validation, J.B., A.D. and I.A.; formal analysis, J.B.; investigation, J.B.; resources, A.D. and I.A.; data curation, J.B.; writing—original draft preparation, J.B.; writing—review and editing, J.B., A.D. and I.A.; visualization, J.B.; supervision, A.D. and I.A.; project administration, A.D. and I.A.; funding acquisition, A.D. and I.A. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Forest Change Initiative (Canadian Forest Service, Natural Resources Canada) and the project Forêt s’Adapter, itself supported by the NSERC (RDCPJ 485153-15), the Ouranos Consortium on Regional Climatology and Adaptation to Climate Change, and the Coop des Frontières.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: All vegetation inventory data are available through SPlot—the Global Vegetation Database (https://www.idiv.de/en/sdiv/working_groups/wg_pool/splot/splot_database.html; accessed on 26 April 2022). Other data presented in this study are available upon request to the corresponding author.

Acknowledgments: We would like to thank Laura Boisvert-Marsh, Patrice Mathieu, Florian Mézerette and Julie Villeneuve for their precious help during field inventories. The input of Laura Boisvert-Marsh and Françoise Cardou during data analysis was also crucial to the success of this study. We would also like to thank Sylvie de Blois, Sylvain Delagrange, Christian Messier and Mark Vellend for their commentaries on the experimental design. We would also like to thank Laura Boisvert-Marsh for editing the manuscript. Accommodations during field inventories were graciously provided by Eva Masson, Samuel Royer-Tardif and Florence Tauc.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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