ORIGINAL PAPER

Phylogenetic attributes, conservation status and geographical origin of species gained and lost over 50 years in a UNESCO Biosphere Reserve

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Abstract

Global change has been occurring at unprecedented rates throughout the last century. A source of recent heated debate has been how such global changes, including land transformation, affect species richness and ecosystem functioning. Growing scientific consensus suggests that more diverse communities support greater ecosystem functioning; however, species numbers might fluctuate over time, and ecosystem processes are shaped by both species richness and species identities. In recent decades, habitat loss and major biodiversity change has occurred on the edge of urban centres because of land transformation to suburban development. Biological surveys provide a valuable record of how biodiversity has responded to this habitat transformation, especially if they have been conducted in the same location over time. Here, we examine changes in species richness, composition and phylogenetic structure between two surveys of vascular plants conducted over 50 years apart on Mont St. Hilaire, Québec, Canada—a UNESCO Biosphere Reserve surrounded by residential development. We found 198 more species in the more recent survey, but failed to detect 70 species that had been recorded in the earlier survey. A significant number of species gains were closely-related introduced non-native species. Species found only during the first survey (species losses) were frequently native species of special conservation status, and these species tended to be more evolutionarily distinct than species gained. Our results demonstrate that, in a UNESCO Biosphere Reserve, there have been significant changes in species richness and composition over the last half-century that might have far-reaching effects on ecosystem properties.

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Introduction

Unprecedented rates of global change have been occurring over this last century, largely driven by human-caused alteration of the climate and land transformation (Pereira et al. 2010; Steffen et al. 2011; Gonzalez et al. 2016). The expansion of suburban developments at the periphery of urban centres is a major local pressure transforming and fragmenting natural ecosystems, resulting in significant ecological impacts including habitat loss and changes in species composition (Vitousek et al. 1997; DeStefano and DeGraaf 2003; Fahrig 2003; Nitoslawski et al. 2017; Béliveau et al. 2017). These changing biodiversity patterns might have wide-ranging consequence for ecosystem functioning and the provisioning of ecosystem services, such as supporting genetic diversity in different plant species to buffer against future land use and climate changes, as well as maintaining pollinator populations and air quality (Pereira et al. 2010; Mace et al. 2012; Vellend et al. 2013a). As more native habitats are lost, it is predicted that impacts will be felt at larger regional and continental scales (Vitousek et al. 1997; DeStefano and DeGraaf 2003). However, local trends in species diversity through time are not clear, and have been the subject of recent debate (see Vellend et al. 2013a; Dornelas et al. 2014; Gonzalez et al. 2016). Growing evidence now suggests that, at local scales, species richness might change little, but species identities will be highly altered. In this study, we examine changes in composition of vascular plant species recorded and vouchered during two botanical surveys conducted within a UNESCO Biosphere Reserve surrounded by suburban development in southern Québec, Canada, and evaluate the phylogenetic structure and conservation status of species gains and losses.

Biological surveys have a long history, spanning several centuries, and are a record of the taxonomic exploration of a particular area with the goal of identifying the species that live there (Wheeler 1995; Soberón et al. 1996). Here, we distinguish between biological surveys and the resampling of vegetation plots: while the latter can also be used to study changes in vegetation through time, they represent a sample from a larger population and have more limited areal coverage (e.g. Hudson and Henry 2009; Vellend et al. 2013a, b; Kapfer et al. 2016). Comparing survey results through time is a powerful approach for evaluating biodiversity change (Stöckli et al. 2011; Elliott and Davies 2014; Morrison et al. 2017; Vellend et al. 2017), and recent advances, including in DNA barcoding (Elliott and Davies 2014), 'BioBlitzes' (Lundmark 2003) and social networking platforms such as iSpot (Snaddon et al. 2013), have increased the number of tools available for conducting large and accurate surveys. Biological surveys allow us to study changes in not only species richness over time, but also species identities and evolutionary relationships, so that we might better understand the impacts of global change on species communities and, potentially, ecosystem functioning (O'Connor and Crowe 2005; Cadotte and Davies 2010).

In the last few decades, information on the phylogenetic relationships among species has been incorporated into more traditional studies of species diversity, often by including branch length data separating taxa to quantify their evolutionary differences (Faith 1992; Clarke and Warwick 1998; Cavender-Bares et al. 2004; Webb and Donoghue 2004). This information can then be used as an aid to guide conservation efforts, for example, to maximise the preservation of phylogenetic (i.e. evolutionary) information within protected areas (Faith 1992; Rodrigues and Gaston 2002; Forest et al. 2007). Phylogenetic information can also increase our understanding of the processes structuring biological diversity at the local, regional and global scales (Helmus et al. 2007; Vamosi et al. 2009; Cavender-Bares et al. 2009). Within the commonly used 'community phylogenetics' framework proposed by Webb and colleagues (Webb 2000; Webb et al. 2002), important biotic and

abiotic processes determining species composition might be inferred from patterns of phylogenetic clustering. Similar metrics might also allow us to explore impacts of biodiversity change through time. For example, if species gained at a site are closely related to each other and/or those already present, their addition would result in little gain in phylogenetic diversity. Conversely, if species gained at a site are both distantly related to each other and to those already at the site, we would expect large gains in phylogenetic diversity. Similarly, if species lost from a site are distantly related to those present, concomitant losses in phylogenetic diversity would be large; however, if the species lost are from clades represented by many close relatives, the loss of phylogenetic diversity would be small. Importantly, the evolutionary relationships among species gained or lost at a site might also have consequences for ecosystem functioning, assuming more closely related species are more ecologically similar (Wiens et al. 2010). For example, the replacement of one species by a close relative might have only a small impact on assemblage functional diversity, whereas a species that is replaced by a more distant relative could result in a large change in functional diversity (Cadotte and Davies 2010; Flynn et al. 2011; Srivastava et al. 2012).

In this study, we examine changes in species composition between two botanical surveys conducted within the Mont St. Hilaire Biosphere Reserve, Québec separated by over 50 years (Fig. 1). Since becoming a UNESCO Biosphere Reserve in 1978, suburban development surrounding Mont St. Hilaire has continued to expand such that the reserve now
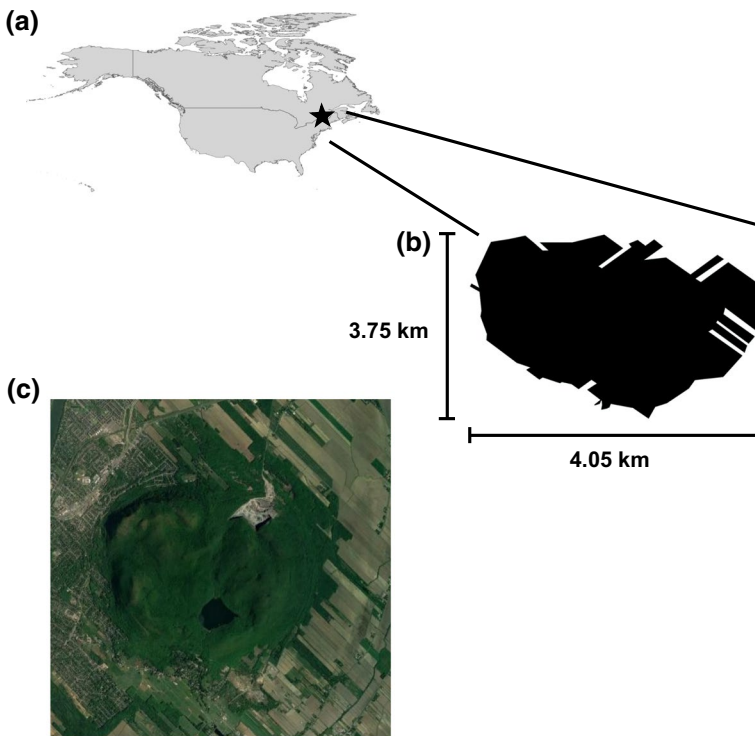
Fig. 1 The location of the Mont St. Hilaire Biosphere Reserve within North America (**a**), as well as reserve boundaries and approximate dimensions (**b**). The map in **c** shows the reserve surrounded by suburban development and agriculture (*Google Maps*, 06 October 2018)

resembles a forest island surrounded by residential development and agriculture (Béliveau et al. 2017). We quantify how species gains and losses are phylogenetically patterned and evaluate their conservation status and geographic origin (native vs non-native). If species gains represent non-native introductions, we might predict that these species will be closely related to each other (although they might be evolutionary distant to the native species pool), reflecting shared traits that might have favored their introduction and persistence. If losses are caused by external drivers such as climate change, then they might also show phylogenetic clustering, assuming that the association between niche traits and the environment is phylogenetically conserved. On the other hand, if species losses represent stochastic population variation, they might show little phylogenetic structure, and species of conservation concern—those with small population sizes and limited distributions—might be most vulnerable to extirpation.

Methods

Sampling

Sampling was conducted in the Mont St. Hilaire Biosphere Reserve (hereafter referred to as the MSH Biosphere Reserve)—a 1000 ha reserve situated on one of the eight Monteregian Hills of the St. Lawrence Lowlands in southern Québec (Maycock 1961; Elliott and Davies 2014). Protection of this regional diversity hotspot goes back to the 1600s, and it is currently recognized as a UNESCO Biosphere Reserve (Maycock 1961; Francis 2004; White et al. 2011), with an old growth forest dominated by the deciduous tree species sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and northern red oak (*Quercus rubra*) (Gilbert and Lechowicz 2004). Invasive species management within the reserve tends to focus on a few key species (e.g. *Phragmites australis* and *Reynoutria japonica* var. *japonica*) (Gault Nature Reserve of McGill University 2018). In recent decades, the region has experienced increases in average mean surface air temperatures (Savage and Vellend 2014; Vincent et al. 2015) and deer populations (Huot and Lebel 2012). Considerable population growth from suburbanization has occurred in the area surrounding the MSH Biosphere Reserve over the past 60 years as a result of its proximity to the metropolitan area of Montréal (Béliveau et al. 2017). Alongside this growth in the regional population, the number of visitors to the MSH Biosphere Reserve has increased; for example, there was over a threefold increase in the number of visitations between 1995 and 2016 (Beauséjour et al. 2015; Gault Nature Reserve of McGill University 2018). To accommodate growing visitor numbers and demands, the trail network, road and building infrastructure within the reserve's boundaries has also expanded since 1960 (Beauséjour et al. 2015; Gault Nature Reserve of McGill University 2018).

During the growing seasons of 2012–2015 (late April to September), we attempted to collect voucher specimens of every terrestrial vascular plant species within the reserve's boundaries using existing lists, herbarium specimens and consultations with other botanists to guide sampling (for details see Elliott and Davies 2014). We did not collect physical vouchers for seven species that were considered rare to the region or reserve to prevent decimating populations: bristly sarsaparilla (*Aralia hispida*); Hitchcock's sedge (*Carex hitchcockiana*); narrow triangle moonwort (*Botrychium lanceolatum* subsp. *angustisegmentum)*; spotted coralroot (*Corallorhiza maculata*); pink lady's-slipper (*Cypripedium*

acaule); green adder's-mouth (*Malaxis unifolia*) and large purple fringed orchid (*Platanthera grandiflora*); however, we recorded geolocations and digital images for these species.

To examine shifts in plant diversity over time, we compared our terrestrial vascular plant survey results to those from a study conducted within the MSH Biosphere Reserve's boundaries during the summer of 1959 and most of the 1960 growing season (Maycock 1961), referring back to the historical specimens vouchered at the McGill Herbarium (MTMG) and the Marie–Victorin Herbarium (MT). The reserve's boundaries have been modified slightly since the initial survey by Maycock (Maycock 1961; Béliveau et al. 2017); we therefore took care to compare collections within matching geographical coordinates. Each historical voucher was revisited to verify whether species identifications had been annotated since the original study, and to ensure that identifications were consistent between the two studies. Species circumscriptions followed published volumes of *Flora of North America* (FNA; Flora of North America Editorial Committee 1993) and *Field Manual of Michigan Flora* for those taxa not yet included in publicly-available FNA treatments (Reznicek and Voss 2012). The current names and authorities of the species collected for this project (see Supplementary Material) are in accordance with VASCAN (Brouillet et al. 2013).

Phylogenetic reconstruction

We reconstructed a dated phylogeny for the reserve's flora using molecular sequence data and multiple fossil calibrations. The species pool for the phylogenetic reconstruction included those species collected during either botanical survey (Supplementary Material). We conducted the phylogenetic analyses using maximum likelihood (ML) and Bayesian inference, with 11 lycophyte taxa as the outgroup and gene sequences from two plastid (*rbcL* protein coding region and *makK* coding region) and two nuclear ribosomal spacers (ITS1 and ITS2). A more detailed description of the methods used for the phylogenetic reconstruction is given in Supplementary Materials 2–6. The phylogenetic reconstruction generated and analysed during the current study is available in the TreeBASE repository, [http://purl.org/phylo/treebase/phylows/study/TB2:S23748]. Additional phylogenetic reconstructions (e.g. the Bayesian posterior distribution) are available from the corresponding author upon reasonable request.

Classification of species

Species found in either or both surveys were classified based on three sets of criteria: (1) a temporal comparison of survey results; (2) their conservation status; and (3) their distribution status in Québec. First, we simply recorded species as either present on both lists (both), found only during the 2012–2015 survey (gains), or found only during 1959–1960 (losses) for the temporal comparison. We then recorded conservation status from lists provided by the Québec provincial government (Développement durable, Environment et Lutte contre les changements climatiques 2017) using the following categories: 'Least concern'—species not susceptible to extirpation from Québec; 'Threatened'—species whose disappearance is anticipated; 'Vulnerable'—species whose survival is at risk even though their disappearance is not anticipated; and 'Susceptible'—species at risk that require special attention. We further grouped species classified under special conservation status (threatened, vulnerable and susceptible) as of conservation concern (CC) due to the low number of species in each of the three categories,

and compared these with species which were not of conservation concern (NCC). Finally, we assessed the distribution status of each species in Québec using VASCAN (Brouillet et al. 2013), and classified species as: present in Québec as a result of natural processes only (native); naturalized in Québec outside of their original range as a result of human activity (introduced); not established permanently in Québec, but re-occurring on a near-annual basis in the wild usually from cultivation (ephemeral); and those reported from Québec but not established or erroneously determined (excluded).

To explore life history correlates of species losses and gains, we further described the species gained or lost during the two surveys according to life span duration (duration) and growth habit (habit), as well as whether the species were forest understory or wetland plants by reviewing species descriptions in *Flora of North America* (FNA; Flora of North America Editorial Committee 1993). For those species not yet included in published versions of the FNA we consulted the following sources, in order: PLANTS Database (USDA 2018), *Manual of Vascular Plants of Northeastern United States and Adjacent Canada* (Gleason and Cronquist 1991) and *Flora Novae Angliae* (Haines 2011). Finally, we recorded the maximum height for each one of the species gained or lost using the resources mentioned above (see Supplementary Material 10) and compared the differences using a two-sample *t* test.

Diversity analyses

Species numbers were first tallied for each of the three classifications described above. We then calculated mean phylogenetic distances (MPD) and mean nearest taxon phylogenetic distances (MNTD) for each category, where MPD is the mean pairwise phylogenetic distance between all species within a category and MNTD is the mean pairwise phylogenetic distance between closest relatives in a category (Webb 2000). The standard effect size of MPD and MNTD was calculated using a null model that maintained species richness within each category but shuffled species identities across categories. Standard effect sizes were multiplied by − 1 to return the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI), respectively. Positive NRI and NTI values indicate phylogenetic clustering, whereas negative values represent phylogenetic overdispersion (Webb 2000). In addition, we calculated the standard effects sizes of the phylogenetic diversity (PD)—the sum of the branch lengths joining all species within a category (Faith 1992)—using an equivalent null model. Finally, we calculated the average evolutionary distinctiveness of species within each category using the equal splits metric of Redding and Mooers (2006). We conducted all analyses across 100 randomly selected phylogenetic trees drawn from the posterior distribution of the Bayesian phylogenetic analysis using the Picante R-library (Kembel et al. 2010).

To evaluate patterns of species loss and gains we conducted two phylogenetic binomial logistic regressions using the phylolm() function in the phylolm R-library (Ho and Ané 2014). In the first analysis, we examined whether gains to the MSH Biosphere Reserve's plant list were related to whether species were native (1) or introduced (0). We removed the two species classified as excluded from this and related analyses. In the second analysis, we investigated whether losses to the reserve's plant list were related to a species conservation status, coding NCC species as 0 and CC species as 1. All analyses were conducted across 100 randomly selected phylogenetic trees drawn from the posterior distribution of the Bayesian phylogenetic analysis.

Results

Temporal changes in species list

A total of 683 vascular plant species, representing 41 orders and 99 families, were included in the 2012–2015 and 1959–1960 surveys of the MSH Biosphere Reserve (Maycock 1961), after correcting for differences in species identifications due to factors such as synonymy and changing species delimitations (Supplementary Material). Of the 683 species, 613 were recorded in the 2012–2015 survey and 485 were recorded in the 1959–1960 survey. The 2012–2015 survey recorded additions to 48 families and species losses in 31 families. Species gains were most notable (ten or more species additions) within the Asteraceae, Cyperaceae and Poaceae; whereas species losses were more common (six to ten species lost) within the Ericaceae, Orchidaceae and Rosaceae (Table 1).

The evolutionary structure of surveyed species differed between collections. Species collected only during the later survey (gains) were phylogenetically clustered—more related than expected by chance (NRI: 2.79 ± 0.05; Figs. 2a, 3a). In contrast, we found species collected only during the earlier survey (losses) did not show significant patterns in NRI (Figs. 2a, 3a), although there was some evidence for phylogenetic clustering when considering only their nearest phylogenetic neighbours (NTI: 1.78 ± 0.03; Fig. 2a and Supplementary Material). Evolutionary distinctiveness was highest for losses (ED: 54.99 ± 9.66, Fig. 3d), and lowest for gains (ED: 39.84 ± 7.18, Fig. 3d), indicating that the species found only during the earlier survey captured more unique phylogenetic diversity than species found only in the later survey.

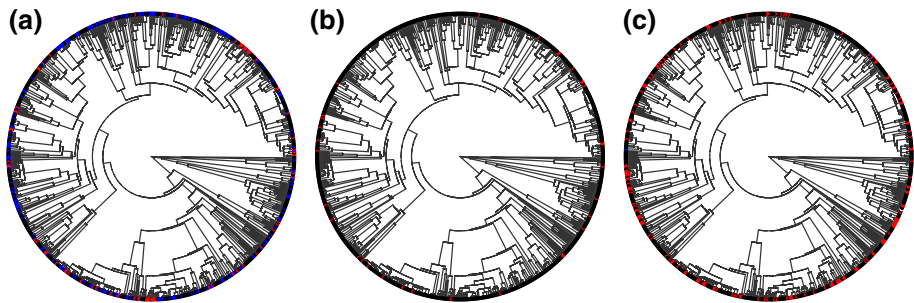## Conservation and Québec distribution

The majority of the species (650 species) surveyed were classified as not of conservation concern (NCC), but 33 plant species (~5%) were classified as of conservation concern (CC: Susceptible, Threatened or Vulnerable in Québec). Losses were significantly more likely to be classified as CC (phylogenetic binomial logistic regression: estimate = 1.85, SE = 0.39, $z = 4.79$, $P < 0.001$; Table 2), and CC species showed a trend towards phylogenetic overdispersion (NRI: -1.02 ± 0.13; Figs. 2b, 3b). In contrast, species classified as NCC tended to be phylogenetically clustered (NRI: 2.10 ± 0.03; Figs. 2b, 3b). On average, species classified as CC were also more evolutionary distinct than species classified as NCC (ED: 66.34 ± 14.08 and 47.26 ± 8.92 for CC and NCC species, respectively; Fig. 3e).

The combined list from the two surveys was composed primarily of species native to Québec (526 species); however, introduced species made up approximately 22.6% (154 species) of the list. Introduced species represented a significant number (~24%) of species gains to the reserve (phylogenetic binomial logistic regression: estimate = − 1.79, SE = 0.20, $z = -8.37$, $P < 0.001$; Table 2), and were phylogenetically clustered (NRI: 6.78 ± 0.09; Figs. 2c, 3c). Native species, on the other hand, showed significant phylogenetic overdispersion (NRI: -4.56 ± 0.04; Figs. 2c, 3c). Evolutionary distinctiveness was similar for native and introduced species (ED: 48.20 ± 9.70 and 47.04 ± 7.33 for native and introduced species, respectively; Fig. 3f).

Table 1 Vascular plant families represented by species gains and losses in the 2012–2015 survey compared to the list published in Maycock (1961)

| Number of different species	Gains	Losses
1	Amaranthaceae, Anacardiaceae, Aspleniaceae, Campanulaceae, Cannabaceae, Celastraceae, Colchicaceae, Convolvulaceae, Fagaceae, Hydrangeaceae, Hypericaceae, Iridaceae, Oleaceae, Onagraceae, Orchidaceae, Orobanchaceae, Phytolaccaceae, Polemoniaceae, Sapindaceae, Typhaceae, Urticaceae, Violaceae, Vitaceae, Xanthorrhoeaceae	Adoxaceae, Amaranthaceae, Amaryllidaceae, Apiaceae, Aspleniaceae, Berberidaceae, Campanulaceae, Caryophyllaceae, Cornaceae, Cupressaceae, Mulluginaceae, Ophioglossaceae, Polygonaceae, Staphyleaceae, Taxaceae, Violaceae
2	Adoxaceae, Apiaceae, Boraginaceae, Equisetaceae, Grossulariaceae, Lycopodiaceae, Pinaceae, Solanaceae	Boraginaceae, Brassicaceae, Caprifoliaceae, Cyperaceae, Hypericaceae, Isoetaceae, Lycopodiaceae, Onagraceae, Poaceae, Primulaceae
3	Euphorbiaceae, Polygonaceae, Primulaceae, Ranunculaceae, Rubiaceae	Ranunculaceae
4	Caprifoliaceae, Dryopteridaceae, Juncaceae, Lamiaceae	
5	Plantaginaceae, Salicaceae	Asteraceae
6–10	Brassicaceae, Caryophyllaceae, Fabaceae, Rosaceae	Ericaceae, Orchidaceae, Rosaceae
11–20	Asteraceae	
21+	Cyperaceae, Poaceae	

Fig. 2 Phylogenetic relationships among the vascular plant species surveyed within the Mont St. Hilaire Biosphere Reserve, Québec showing temporal changes in the species list (**a**), conservation status (**b**) and their distribution status in Québec (**c**). In (**a**), black tip labels represent species present on both lists, whereas blue and red tips show species found only in the 2012–2015 survey and those found only in the 1959–1960 survey, respectively. In (**b**), species not of Conservation Concern (NCC) are shown in black, whereas species of Conservation Concern (CC) are in red. In (**c**) native species are indicated by black, ephemeral by white, excluded by blue and introduced species by red tip labels. (Color figure online)

Growth characters and habitat preferences

Most species gained and lost during the two surveys were perennial herbs (Table 3). Notably, losses comprised a greater proportion of perennial to annual species than gains (6.67:1 and 3.61:1; proportion of perennial to annual species, for losses and gains respectively). Furthermore, the proportion of woody tree and shrub species relative to non-woody herbs and vines was higher for losses compared to gains (0.24:1 and 0.19:1; proportion of woody to non-woody species, for losses and gains respectively). Also of note, the proportion of understory plants relative to non-understory plants found only in the earlier survey was higher (1.38:1) compared species found only in the later survey (0.60:1), as well as the proportion of wetland plants to non-wetland plants (0.64:1 for losses compared to 0.47:1 for gains). Finally, although the mean maximum height was slightly lower for species losses compared to gains (1.64 m for losses vs 2.33 m for gains), the values were not significantly different (two-sample t-test, $t = 1.56$, df $= 241.9$, $P = 0.12$).

Discussion

We compared the changes in species richness, composition and evolutionary relationships of plants within the Mont St. Hilaire Biosphere Reserve (MSH Biosphere Reserve) between two time periods: 1959–1960 and 2012–2015. We documented 198 more species in the more recent survey, of which 58 had not been previously recorded in the reserve. However, we also failed to detect in the more recent survey 70 species that were recorded historically. A significant proportion of additions (gains) were introduced species, while species found only during the first survey (losses) were often species of special conservation concern. Gains to the reserve's list were more closely related to each other than expected by chance and more likely to be annuals, suggesting they came from a few select clades that might share traits that facilitated their establishment. Losses were not phylogenetically structured, but species lost tended to be more evolutionarily distinct than species gained and more often associated with the forest understory and wetland habitats. Our
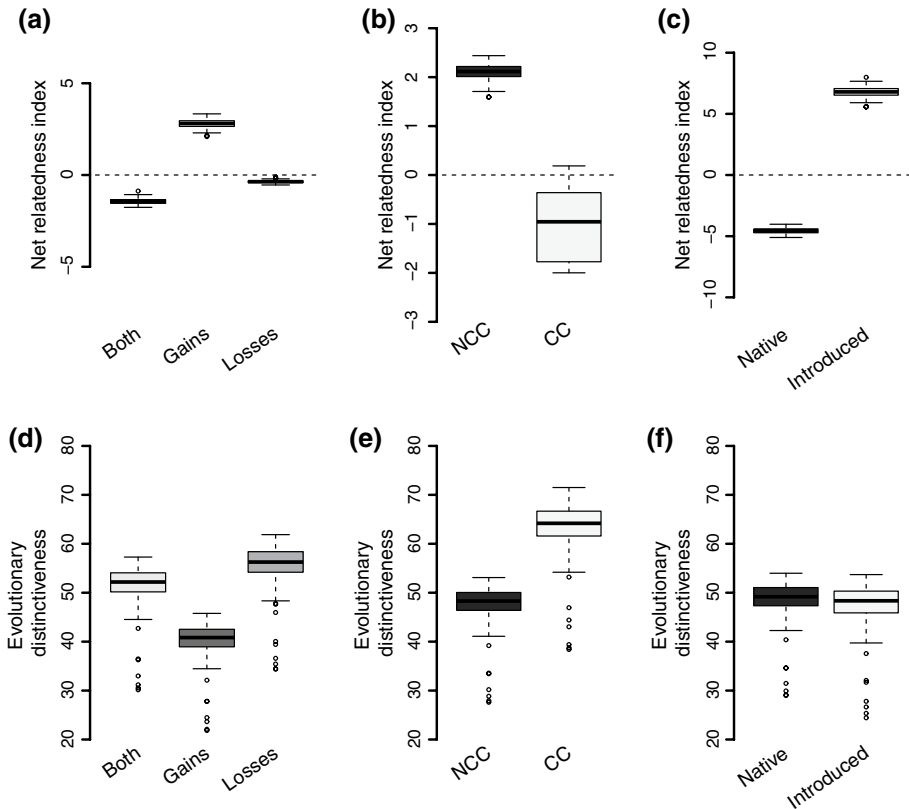
Fig. 3 Net relatedness index and evolutionary distinctiveness of species sampled from the Mont St. Hilaire Biosphere Reserve (**a**, **d**), conservation status of species (**b**, **e**) and their distribution status in Québec (**c**, **f**). Abbreviations for conservation status are: conservation concern (CC) and not of conservation concern (NCC). All values were standardized using a null model that randomized species richness and calculations were conducted across a Bayesian posterior distribution of 100 randomly selected phylogenetic trees. Boundaries for each boxplot show the 25th and 75th percentiles, medians are represented by thick lines and whiskers above and below represent the 10th and 90th percentiles. Empty circles indicate outlying data

results suggest a process of biological homogenization is reshaping the flora of the MSH Biosphere Reserve, and that there is a danger that native species of conservation concern are at risk of local extinction from the site.

Our findings indicate that species richness is increasing within the MSH Biosphere Reserve. Recent debate has focused on whether biodiversity is increasing or decreasing with global change (see Gonzalez et al. 2016; Vellend et al. 2017), with a growing number of studies suggest that species richness increases might be relatively common at local and regional scales (Vellend et al. 2013a; Dornelas et al. 2014). Similar increases in local species richness over the past 35 years have been observed within the adjacent protected areas of Mont Saint-Bruno National Park and Mont-Mégantic. These findings suggest a general trend for increasing richness across the region (Savage and Vellend 2014; Beauvais et al. 2016). Several factors might have contributed to the apparent increase in species richness within the MSH Biosphere Reserve, including dispersal of plant propagules into the reserve by human and animal vectors, changes in species distributions resulting from

Table 2 Phylogenetic binomial logistic regressions on native and conservation status of the vascular plant species surveyed during 1959–1960 and 2012–2015 within the Mont St. Hilaire Biosphere Reserve, Québec

Analysis	Parameter[a]	Estimate	SE	z value	*P value*
Gains ~ natives					
	Intercept	0.29	0.16	1.76	0.08
	Native	− 1.74	0.20	− 8.59	< 0.001
Losses ~ conservation concern					
	Intercept	− 2.26	0.17	− 13.47	< 0.001
	Conservation	1.76	0.39	4.54	< 0.001

Gains ~ natives: phylogenetic binomial logistic regression (estimate = − 1.79 [− 1.81, − 1.77], SE = 0.20 [0.20, 0.20], z = − 8.78 [− 8.86, − 8.70], P < 0.001). Losses ~ conservation concern: phylogenetic binomial logistic regression (estimate = 1.85 [1.82, 1.87], SE = 0.39 [0.39, 0.39], z = 4.79 [4.71, 4.86], P < 0.001)

[a]Parameter estimates shown are estimated on a single sampled phylogenetic tree. Confidence intervals [ ] on slope estimates were also calculated from 100 randomly selected phylogenetic trees from the Bayesian posterior distribution

Table 3 Major growth traits and habitat preferences of plant species gained in the 2012–2015 survey compared to losses from the list published in Maycock (1961)

	Category	Gains	Losses
Duration	Biennial:annual	0.17:1	0.22:1
	Perennial:annual	3.61:1	6.67:1
Growth form	Woody:non-woody	0.19:1	0.24:1
Site preference	Forest understory:other	0.60:1	1.38:1
	Wetlands:other	0.47:1	0.64:1

Woody species include tree and shrub growth forms, while non-woody include herbs and vines

climate change, and changes in tree overstory due to events such as insect outbreaks and ice storms (Hooper et al. 2001; Côté et al. 2004; Gilbert and Lechowicz 2005; Knight et al. 2009; Beauvais et al. 2016).

White-tailed deer (*Odocoileus virginianus*) population levels have been increasing in the region surrounding the MSH Biosphere Reserve in recent decades (Gilbert and Lechowicz 2005; Huot and Lebel 2012; Beauvais et al. 2016) and have appeared to impact the vegetation structure and composition of the reserve by reducing forest understory cover and perhaps facilitating the establishment of annuals at the expense of understory shrubs and other woody taxa. The increase in visitation rates, trail and other infrastructure within the reserve has also likely aided dispersal of plant propagules into the reserve, as human clothes and equipment often serve as effective dispersal vectors (Pickering and Mount 2010; Ballantyne and Pickering 2015). Since the first survey in 1959–1960, several species have expanded their ranges northward as the climate has warmed (Parmesan and Yohe 2003; Parmesan 2006; Chen et al. 2011), and species previously climatically excluded from the reserve are now able to establish viable populations within it. Changes in tree overstory can also alter understory plant composition by affecting the amount of sunlight received by understory plants (Hooper et al. 2001; Darwin et al. 2004; Filion et al. 2006; Savage and Vellend 2014). There is documented evidence of notable canopy changing events

since Maycock's 1959–1960 survey, such as the January 1998 ice storm (Hooper et al. 2001; Darwin et al. 2004); however, the overstory canopy has closed in recent years in the reserve, reducing the amount of sunlight reaching the ground.

Species losses showed only weak phylogenetic clustering, but had relatively high evolutionary distinctiveness compared to species gains, and a majority of losses had special conservation status in Québec (susceptible, threatened or vulnerable). The loss of evolutionarily distinct species is noteworthy as it implies a potential decline in phylogenetic and functional diversity that might be linked to increasing functional homogenization of the reserve's flora, with further consequences of reducing adaptation to future environmental changes (Olden et al. 2004; Cadotte and Davies 2010). Moreover, assuming niche conservatism, the loss of phylogenetic diversity (and thus functional diversity) could additionally alter key ecosystem functions such as biomass production and nutrient flow (Wiens et al. 2010; Flynn et al. 2011; Srivastava et al. 2012). The loss of species with special conservation status is obviously a concern, especially for a biosphere reserve within an agricultural-suburban matrix where natural habitats are increasingly limited.

We note that it remains possible that the species losses observed in our study represent intrinsically rare species and that we simply missed them in our more recent survey. However, because we had the species list from the earlier survey, we actively searched for these 'missing' species, using information from herbarium labels and knowledge from local botanists to help guide us. Thus, we believe many of these losses represent true extirpations from the local flora of the MSH Biosphere Reserve. Possible reasons for these losses include (but are not limited to) stochastic population decline from initial low population numbers, as well as some of the same drivers potentially explaining species gains, such as recent anthropogenic climate change and the increase in deer herbivory that is thought to have impacted many understory herbs in recent decades (White et al. 2011; Beauvais et al. 2016). Disentangling these potential drivers and why some species are favoured while others decline will require further research.

A significant number of species gains were classified as introduced species non-native to Québec. The introduction of non-native species has been shown to have increased plant species richness on islands over recent timescales (Sax and Gaines 2003, 2008) and on continents over longer time frames (Winter et al. 2009). Increases in species richness resulting from the introduction of non-native species are often greater in suburban environments as species composition is altered through the process of biological homogenization (McKinney 2002, 2008; Tait et al. 2005; Rooney et al. 2004). Our results contrast with those from Mont Saint-Bruno National Park and Mont-Mégantic that show that observed increases in species richness over time can be explained by higher numbers of native species, but the processes underlying this pattern can sometimes be unclear (Savage and Vellend 2014; Beauvais et al. 2016). In the case of the MSH Biosphere Reserve, the surrounding suburban area might serve as a repository of non-native plant propagules capable of dispersing into the reserve through vectors such as white-tailed deer (Myers et al. 2004; Gilbert and Lechowicz 2005), or on the many visitors to the MSH Biosphere Reserve; for example, one of our recorded introductions was wheat (*Triticum aestivum*) found growing near a stopping point along a popular hiking trail within the reserve.

We found that species classified as introduced to Québec were more evolutionarily related than expected by chance, whereas native species were less related, although the evolutionary distinctiveness of both groupings was similar. Similar phylogenetic clustering of non-native plant species has been observed elsewhere, but those results were scale-sensitive, with additional processes (e.g. environmental filtering, short-distance dispersal and competition) having stronger effects on species establishment at local scales (Cadotte

et al. 2009). Under the assumption of phylogenetic niche conservatism, the phylogenetic clustering of close relatives observed in our study suggests introduced species might share similar ecological traits—such as high specific leaf area, small seed mass and other dispersal related traits—that might have facilitated their establishment (Wiens 2004; Hamilton et al. 2005; Cadotte et al. 2009).

In our survey, species gains came disproportionately from the Asteraceae, Cyperaceae and Poaceae (>ten species additions coming from each of these families), with 68 (53.1%) of gains from within order Poales ("graminoids": Cyperaceae, Juncaceae and Poaceae families). Several possible reasons explain this taxonomic bias, including changes in the tree canopy and opening of the understory following increased browsing by white tailed deer and a major ice-storm event in 1998. High white-tailed deer densities could be partially responsible for shifting plant understory assemblage composition from shrub to graminoid-dominated within the MSH Biosphere Reserve, as has been reported elsewhere (Rooney 2009). As discussed above, insect outbreaks and ice storms can also change understory plant composition (Hooper et al. 2001; Darwin et al. 2004; Filion et al. 2006; Savage and Vellend 2014), although we do not think these are as important factors in explaining the disproportionately high number of species gains from within order Poales, since the reserve's tree canopy appears to have closed in recent years.

While we believe there has likely been a real increase in the number of species within the MSH Biosphere Reserve from within Poales, there is also a possibility of surveyor bias. The Cyperaceae and Poaceae families are especially speciose and have the reputation among botanists for being difficult to discriminate (Flora of North America Editorial Committee 1993; Christenhusz and Byng 2016). The effect of surveyor bias on plant species richness patterns has also been documented elsewhere (e.g. Oredsson 2000; Sastre and Lobo 2009; Ahrends et al. 2011). It is likely that previous botanical work in the reserve was influenced by the specific training and botanical knowledge of individual researchers. For example, there has been an extensive survey of *Carex* on Mont St. Hilaire (see Bell 2003) since Maycock's original work in 1959–1960, greatly improving the knowledge of the diversity and distribution of Cyperaceae species within the reserve, and this information has been passed on to other botanists working in the area. In addition, the chief botanist working on the most recent survey had specific training in the Poaceae during their early academic and professional career, whereas it seems Maycock and co-workers did not have any particular botanical affinity for the Poales. We note that, for example, Maycock and co-workers collected many specimens of the same relatively common Poaceae species from Mont St. Hilaire (e.g. 10 specimens of drooping woodreed—*Cinna latifolia* were deposited at MTMG), which might indicate that they found identifications confusing for that family of graminoids. The additions from within these species rich families containing many recent divergences might help explain the low evolutionary distinctiveness of species gains in the reserve.

Other possible source of error in comparing floristic surveys comes from changes in taxonomy, species misidentifications and differences in sampling effort. We took care to reduce taxonomic errors by reviewing herbarium specimens and checking names for synonymy to ensure that plants belonging to the same species had not been given different names in the two surveys. While it is almost impossible to replicate an historical survey exactly—for example, number of person days in the field and botanical training can both influence survey results (Ahrends et al. 2011)—we assume, based on the information on Maycock's specimen labels and his former position at McGill University, which owns and manages the reserve, that both surveys involved botanists with ample training and experience with the temperate forest flora. Finally, we reviewed the location information on

the labels of Maycock's specimens to check that the two surveys encompassed the same geographical extent; however, it was impossible to be sure that the two surveys overlapped completely in space since the first survey did not include GPS co-ordinates.

Finally, we note that resource limitations mean that it is not always possible to voucher all species sampled in a survey; we emphasize here how properly accessioned herbarium specimens give added long-term value to this type of botanical work by allowing them to be reviewed by future researchers (Pyke and Ehrlich 2010; Culley 2013). We believe that these specimens will become increasingly important historical records allowing us to better document biodiversity change.

Conclusions

We have shown a net increase in documented species richness over time within the MSH Biosphere Reserve, while considering both changes in species numbers and the role of surveyor bias. Our results indicate that, although the reserve is well-managed and respected as a natural area by local citizens, significant changes in species richness and evolutionary relationships have occurred over the past few decades. The biological homogenization that is likely occurring with the MSH Biosphere Reserve and other reserves in the region (e.g. Mont Saint-Bruno National Park) might have long-term ecological consequences, such as altering ecosystem functioning and services (Mitchell et al. 2015). Recent conservation work focusing on the Montérégie region of southern Québec highlights the importance of forest connectivity on maintaining functional diversity (Mitchell et al. 2015). In response, forest corridors have been proposed and developed for the MSH Biosphere Reserve and surrounding area (Dupras et al. 2015; Béliveau et al. 2017). We argue that a commitment to long-term planning considering ecological principles, such as maintaining phylogenetic and functional diversity, is important at the landscape scale to prevent the loss of native species of conservation concern, and support the valuable ecological services provided by more diverse floras within biological reserves surrounded by encroaching human development.

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